Climate Forcing and Sudden Change in Marine Ecosystems

by

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Our traditional view of natural systems, therefore, might well be less a meaningful reality than a perceptual convenience.

C.S. Holling (1973)

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Abstract

Rationale—Continental shelf ecosystems occasionally undergo "regime shifts" – abrupt reorganization events that can have deleterious social and economic effects on fishing communities that rely on affected species. Regime shifts are often interpreted as transitions to alternative ecosystem states after external perturbations such as fishing pressure cross a critical threshold; they have also been related to shifts in modes of internal climate variability, such as the Pacific Decadal Oscillation and North Atlantic Oscillation. However, hypotheses explaining regime shifts are extremely difficult to test, given the multivariate nature of both stressors and community response, the frequent paucity of data at adequate spatial and temporal scales, possible non-linear and non-stationary relationships, and the use of observational data that preclude strong inference. Furthermore, regime shifts have often been invoked to explain ecological change without the consideration of competing models, such as the accumulation of more gradual change over time. As a result, both the nature of community-level biological change in continental shelf systems (regime shifts vs. more gradual change), and the identity of factors producing observed change, remain poorly resolved. Given increasing anthropogenic disturbance to continental shelf ecosystems globally, there is a need both for better understanding of the dynamics underlying sudden ecological change, and for tools providing early detection of ecosystem change to allow for proactive management measures that might minimize associated socio-economic disruption. Finally, the regime shift concept is largely based on work in North Atlantic and North Pacific ecosystems, and there is a need for studies in other areas to determine if the regime shift model is widely applicable.

Approach—In many continental shelf systems, long-term biological observations that are necessary for testing hypotheses concerning decadal-scale ecological change are extremely limited. The first four chapters of this thesis use the northeast Pacific as a model system, as this region is home to one of the best extant datasets of long term, large-spatial scale biological observations globally. I compiled a set of 38 climatic time series (regional climate parameters and large-scale indices) and 78 biological time series (mostly production or abundance estimates for

commercially-important fish and invertebrate populations), from the 1960s to the present, covering the continental shelf between 30°N and 65°N. This dataset allowed me to evaluate internal climate variability, commercial fishing and incremental climate change as factors explaining decadal-scale biological variability (Chapter 1); test competing models of gradual change and regime shifts for explaining decadal-scale ecological variability (Chapter 2); develop an approach for evaluating possible ecosystem shifts at the ends of time series (Chapter 2); test for non-stationary biological responses to climate perturbations (Chapter 3); and test statistical tools for early detection of ecosystem transitions (Chapter 4). In Chapter 5 I use the methodology developed in the previous chapters to evaluate a data-poor situation in southeast Australian continental shelf ecosystems, using nine climatic and 12 biological time series (seabird reproductive parameters and recruitment estimates for commercially-important fish stocks) for the period 1967-present. This chapter tested competing hypotheses invoking secular change and regime shifts to explain regional climate-biology covariation.

Results—Analysis of northeast Pacific data showed that: the ecological change that is frequently related to regime shifts in the literature is in many instances better described as the result of incremental change over time (Chapters 1 and 2); commonly held assumptions concerning the dominant role of internal climate variability as an external driver on the system are poorly supported by data (Chapters 1 and 2); assessment of incipient ecosystem shifts may be supported both by model-derived statistical indicators and by formal evaluations of the length of observation needed to evaluate ecosystem state (Chapters 2 and 4); and assumptions of stationarity are inadequate for understanding community responses to climate variability (Chapter 3). In southeast Australia (Chapter 5), I found that secular change best described decadal-scale climatic and biological variability, with little evidence for a role of regime shift-type variability in the system.

Conclusions—My findings from the northeast Pacific suggest several revisions to current understanding of decadal-scale variability in continental shelf ecosystems. Even in ecosystems that are generally free of overfishing and heavily loaded by leading modes of global climate variability, anthropogenic drivers (fishing, secular climate change) are at least as important as climate variability as agents of ecological change. Furthermore, gradual change over time is at least as important to consider as more obvious regime shifts when analyzing decadal-scale ecological variability. The

tests of early indicators for sudden change included in this thesis are the first application of these proposed methods to actual fisheries management data, and demonstrate their potential usefulness in this context. Finally, while my findings confirmed the importance of secular change in southeast Australian ecosystems, analysis of northeast Pacific data shows that the small sample of biological time series in Chapter 5 is likely to produce an underestimate of the complexity of temporal variability in the system.

Introduction

Biological populations and communities are complex systems that may undergo sudden transitions between alternative stable states. The importance of alternative states in ecology, and the thresholds and discontinuities separating them, was established during the 1960s and 1970s (Lewontin 1968, Holling 1973, May 1977), though, as is the case with many concepts in ecology, precedents may be found further back in the literature (e.g., Lotka 1956). Alternative stable states are characterized by: 1) dramatic differences in state characteristics (e.g., density or reproductive success for populations, species composition and trophic structure for communities, human services for ecosystems); 2) different sets of internal and external factors regulating the system; and 3) hysteresis, or critical perturbation thresholds for transitions between states that depend on the direction of change in the perturbation parameter (Scheffer et al. 2001, Beisner et al. 2003). Understanding and predicting switches between alternative states have become leading research topics in ecology (Scheffer and Carpenter 2003, Scheffer et al. 2012).

Continental shelf communities occasionally undergo abrupt, profound transitions. Historical examples include coherent changes across populations of salmon (*Oncorhynchus* spp.), groundfish, small pelagic fishes and invertebrates in the northeast Pacific in the late 1970s (Hare and Mantua 2000); the collapse of cod (*Gadus morhua*) and other groundfish populations, and coincident booms in elasmobranchs, decapod crustaceans and small pelagic fishes, in the northwest Atlantic in the 1980s (Link et al. 2002, Choi et al. 2004); and shifts, in the 1980s, in North Sea phytoplankton and zooplankton phenology and community composition, and recruitment success for a variety of demersal and pelagic fishes (Beaugrand 2004). Because these transitions involve abrupt, persistent change to dominant fish and invertebrate populations, they quickly propagate into the social and economic life of fishing communities (Hamilton et al. 2003, Hamilton et al. 2004). Indeed, though these abrupt transitions are most often studied as problems in ecology, with no explicit consideration of the implications for humans, fisheries catches are potentially both explanatory variables (Choi et al. 2005, Fauchald 2010) and response variables (Hare and Mantua 2000, Collie et al. 2013) in these ecosystem transitions,

underscoring the importance of these transitions as a problem in applied marine ecology applications, such as fisheries management.

Though alternative stable state theory has a long history in ecology, the phenomenon remains best-studied in models (van Nes and Scheffer 2004, van Nes and Scheffer 2007) and in simple ecosystems, notably shallow freshwater lakes (Scheffer and van Nes 2007). Sudden transitions in continental shelf ecosystems have long been offered as a possible example of alternative stable states in large, complex ecosystems (Scheffer et al. 2001, Scheffer and Carpenter 2003), and there has been interest by oceanographers and marine ecologists in applying alternative stable state theory to understanding sudden transitions in marine systems (Choi et al. 2004, Collie et al. 2004, Mantua 2004). However, progress along these lines remains slow. Problems include the paucity of data at suitable spatial and temporal scales, the use of observational data sets that are open to alternative interpretations (e.g., Frank et al. 2013, Greene 2013), the time (years to decades) needed to distinguish persistent states from transitory reactions to perturbation (Frank et al. 2011), and the complexity of multivariate processes in marine systems with unknown variables and relationships (Overland et al. 2008). As a result of these difficulties, the question of whether alternate stable state theory is applicable to abrupt reorganization events in continental shelf ecosystems remains unanswered (Möllmann and Diekmann 2012), just as it remains unanswered in much more tractable intertidal and nearshore demersal ecosystems (Connell and Sousa 1983, Petraitis and Dudgeon 2004, Dudgeon et al. 2010).

The difficulty in applying theory to understanding the dynamics of these systems is further underscored, and exasperated, by inconsistent use of terminology. The concept of a "regime shift" was first applied to terrestrial ecosystems (Noy-Meir 1975), and then applied to persistent shifts in northeast Pacific communities associated with the Pacific Decadal Oscillation climate pattern (Brodeur et al. 1996, Minobe 1997). In spite of becoming widespread in oceanography and marine ecology, the term never achieved a uniform definition in these fields (Lees et al. 2006, Overland et al. 2008). The term was subsequently adopted by ecologists to refer specifically to threshold transitions between alternative states. Thus, in marine ecology a "regime shift" may be any abrupt change in a time series (Andersen et al. 2009), while in general ecology, the term is most often applied specifically to catastrophic shifts between alternative states (Biggs et al. 2009, Carpenter et al. 2011).

As an alternative to stable state theory, another point of view holds that abrupt reorganizations of continental shelf ecosystems are driven by sudden changes in leading modes of internal climate variability (Mantua et al. 1997, Minobe 1997, Hollowed et al. 2001, Greene et al. 2008, Greene et al. 2013). Since red noise variability may produce decadal-scale periods when climate parameters depart from their long-term mean (Rudnick and Davis 2003, Overland et al. 2006), a linear ecological response to internal climate variability, perhaps dampened by the generation time averaged across the community, might provide a more parsimonious explanation for sudden ecosystem shifts than alternate stable state theory (Hsieh and Ohman 2006, Di Lorenzo and Ohman 2013). However, abrupt community shifts may also result from Gaussian climate variability coupled with non-linear biological dynamics that are consistent with alternative stable states (Hsieh et al. 2005, Deyle et al. 2013). The underlying dynamics remain uncertain.

There is widespread expectation that increased anthropogenic disturbance, most notably through climate change, fishing, eutrophication and habitat destruction, is making sudden ecosystem transitions more frequent (Folke et al. 2004). A stronger theoretical underpinning would provide an important step towards understanding these events, and theory has recently been developed to provide generic early warning tools for sudden ecosystem transitions (Scheffer et al. 2009, Kéfi et al. 2013). However, these approaches have so far been tested in models (Carpenter and Brock 2006, Guttal and Jayaprakash 2008), laboratory microcosms (Drake and Griffen 2010) and small ecosystems amenable to experimental manipulation (Carpenter et al. 2011); their utility in large, open ecosystems, such as those on continental shelves, remains largely untested (Scheffer et al. 2012).

The primary goal of this thesis it to improve empirical understanding of dramatic shifts in continental shelf ecosystems by confronting theoretical predictions and competing models with data from the northeast Pacific. This ocean basin is distinguished by a relative abundance of high-quality, decadal-scale biology time series, which allow for rigorous hypothesis testing. A secondary goal is to apply methodology from the northeast Pacific to elucidate patterns of decadal-scale ecosystem variability in southeast Australian continental shelves, a relatively data-poor system.

In the order in which they are presented, the specific questions addressed by the thesis are:

Chapter 1) *What are the set of external perturbations driving abrupt shifts?* As is the case with most questions in ecology, the answer is likely to be contingent on system- and time-dependent factors (Lawton 1999). However, northeast Pacific ecosystems (i.e., the California Current, Gulf of Alaska and eastern Bering Sea large marine ecosystems [LMEs]) provide an excellent case study for answering this question. While internal climate variability has long been associated with decadal-scale variability in these ecosystems (Trenberth and Hurrell 1994, Mantua et al. 1997, Minobe 1997), the seminal studies documenting the ecological importance of internal climate variability often made no attempt to test statistical hypotheses explaining observed ecosystem changes (Hollowed and Wooster 1992, Mantua et al. 1997, Anderson and Piatt 1999). This was understandable given the statistical techniques and computing power that were generally available in the 1990s (Daskalov et al. 2003), but even with advances in those fields, studies continue to invoke internal climate variability as a leading driver of decadal-scale, community-level biological change, without examining competing hypotheses invoking factors such as secular change in climate or commercial fishing (e.g., Francis and Hare 1994, Mantua et al. 1997, Anderson and Piatt 1999, Hare and Mantua 2000, Beamish et al. 2004, Litzow 2006, Kaeriyama et al. 2009). This chapter uses updates to previously-published biological time series from two northeast Pacific LMEs (Gulf of Alaska and eastern Bering Sea) to examine the importance of internal climate variability, secular climate change and commercial fishing as drivers of community-level biological change from 1965-present. Overfishing and extensive habitat loss for anadromous fishes in the California Current LME (Nehlsen 1997, Harvey et al. 2006) were judged too difficult to account for in statistical models, so data from that ecosystem were excluded from this chapter.

Chapter 2) *Is decadal-scale ecological variability best described by models invoking sudden shifts, or gradual change? How can we determine whether a jump in observed ecosystem parameters represents short-term variability or the onset of a new, persistent pattern?* This chapter again uses northeast Pacific data (in this case, from all three LMEs). The northeast Pacific serves as an excellent case study for the widespread problem of sudden shifts being asserted by ecologists without the consideration of competing models invoking more gradual ecological change

(Spencer et al. 2012). Although a number of incremental forcing mechanisms are at work in the northeast Pacific (e.g., secular climate change, persistant fishing removals, habitat loss; Nehlsen 1997, Gillett et al. 2003, Harvey et al. 2006, Schwing et al. 2010), making the presence of persistent, incremental ecological change a reasonable expectation, comparisons of gradual and abrupt models for ecological change across the region have not been previously published. Additionally, after the dramatic region-wide ecological transition that accompanied the 1976/77 shift in the PDO (Anderson and Piatt 1999, Hare and Mantua 2000, Benson and Trites 2002), there has been a history of attempts to provide early recognition of subsequent shifts in this region (e.g.; Bond et al. 2003, Peterson and Schwing 2003, Hatch 2013). However, in spite of the advancement of statistical techniques to test for shifts at the ends of time series (e.g., Rodionov 2006), many years of data after a putative shift are required to distinguish interannual noise from low-frequency variability (Litzow 2006). This chapter presents a formal approach for assessing the length of observation needed for evaluating potential shifts.

Chapter 3) *Do continental shelf communities show non-stationary responses to perturbations such as climate change and fishing?* Non-stationary relationships with external variables are a hallmark of alternate stable state theory (Scheffer et al. 2001, Beisner et al. 2003). Recent work in the northeast Pacific has produced a number of examples of populations that are controlled by different sets of external and internal factors at different points in time, producing correlations with individual driver parameters that arise and disappear (Ciannelli et al. 2004, Ciannelli et al. 2005, Litzow and Ciannelli 2007, Bacheler et al. 2012, Ciannelli et al. 2012, Sugihara et al. 2012, Deyle et al. 2013). However, little (or no) research has been published on non-stationary relationships between regional community variability and external drivers. By applying a model-selection approach (Burnham and Anderson 2002) using threshold generalized additive models that fit non-parametric and non-stationary driver-response relationships, I test for non-stationary community responses to perturbations of northeast Pacific ecosystems.

Chapter 4) *Can generic regime shift indicators predict the collapse of commercially exploited populations?* The suggestion that "generic" statistical indicators, such as rising variance and rising skewness in key system parameters over time, might predict an increased likelihood of a sudden shift in system properties, has sparked substantial research interest in recent years (Scheffer et al. 2009). While

generic indicators suggest an avenue for deriving useful fisheries management tools from ecological theory, the idea is in its infancy, with empirical tests to date mostly limited to laboratory microcosms and simple, easily manipulated ecosystems, with few tests in the large, open ecosystems that are the purview of fisheries management (Scheffer et al. 2012). This chapter uses a set of historical catch data from 14 crustacean fisheries in Alaska, running from the 1960s to the 2000s, to test for the presence of proposed indicator behaviors (increasing spatial variance and skewness in catch) prior to stock collapse.

Chapter 5) *Can approaches from the North Pacific be applied to understand ecological variability in a data-poor situation?* The first four chapters of the thesis are concerned with LMEs where a relatively large number of biological time series of duration approaching 50 years are available for analysis; even in this enviable situation, statistical power is often barely sufficient for testing theoretical predictions in the presence of the noise that is pervasive in real ecosystems. Is there any hope for detecting sudden ecosystem shifts in more typical data-limited situations? This question is addressed with data from southeast Australian marine ecosystems, which are experiencing a suite of rapid physical changes associated with the southward incursion of the East Australia Current (Suthers et al. 2011). While pervasive community responses to these physical changes have been documented in intertidal and nearshore benthic communities (e.g., Ling 2008, Pitt et al. 2010), the scarcity of available data has precluded a full understanding of the nature of biological response in pelagic communities (Johnson et al. 2011). Using 12 time series of long-term biological observations (seabird reproductive parameters and fish recruitment estimates; 1967-2010), this chapter seeks to define biological responses in the presence of simultaneous patterns of secular and abrupt climate variability. A further goal is to evaluate the ability to detect complex, non-linear trends in community variability in a data-poor situation compared with a data-rich situation such as that in the northeast Pacific.

<u>Chapter 1</u> Reassessing regime shifts in the North Pacific: incremental climate change and commercial fishing are necessary for explaining decadal-scale biological variability

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Abstract

In areas of the North Pacific that are largely free of overfishing, climate regime shifts – abrupt changes in modes of low-frequency climate variability – are seen as the dominant drivers of decadal-scale ecological variability. We assessed the ability of leading modes of climate variability (PDO, NPGO, AO, PNA, NPI, ENSO) to explain decadal-scale (1965-2008) patterns of climatic and biological variability across two North Pacific ecosystems (Gulf of Alaska and Bering Sea). Our response variables were the first principle component (PC1) of four regional climate parameters (SST, SLP, freshwater input, ice cover) and PCs 1-2 of 36 biological time series (production or abundance for populations of salmon [*Oncorhynchus* spp.], groundfish, herring [*Clupea pallasii*], shrimp and jellyfish). We found that the climate modes alone could not explain ecological variability in the study region. Both linear models (for climate PC1) and generalized additive models (for biology PC1-2) invoking only the climate modes produced residuals with significant temporal trends, indicating that the models failed to capture coherent patterns of ecological variability. However, when the residual climate trend and a time series of commercial fishery catches were used as additional candidate variables, resulting models of biology PC1-2 satisfied assumptions of independent residuals and out-performed models constructed from the climate modes alone in terms of predictive power. As measured by effect size and Akaike weights, the residual climate trend was the most important variable for explaining biology PC1 variability, and commercial catch the most important variable for biology PC2. Patterns of climate sensitivity and exploitation history for taxa strongly associated with biology PC1-2 suggest plausible mechanistic explanations for these modeling results. Our findings suggest that, even in the absence of overfishing and in areas strongly influenced by internal climate variability, climate regime shift effects can only be understood in the context of other ecosystem perturbations.

Introduction

Red noise in leading modes of internal climate variability may produce "square wave" behavior consisting of abrupt switches between steady states (Minobe 1999, Rudnick and Davis 2003, Di Lorenzo and Ohman 2013). Recognition of abrupt shifts in leading modes of basin-scale climate variability (hereafter "climate regime shifts") was a major advance in marine ecology, as these events explain biological variability that is coherent at very large spatial scales, such as inverse patterns of salmon (*Oncorhynchus* spp.) production in the northern and southern Northeast Pacific and inverse patterns of sardine (*Engraulis* spp.) and anchovy (*Sardinops* spp.) production in a variety of temperate ecosystems (Mantua et al. 1997, Francis et al. 1998, Chavez et al. 2003). Climate regime shifts are expected to continue under anthropogenic climate change (Overland and Wang 2007), and understanding the impacts of these shifts relative to anthropogenic climate change and other anthropogenic impacts, such as fishing, is vital for understanding and managing marine ecosystems.

However, while anthropogenic climate change has the potential to modify the impacts of internal climate variability, very few studies have attempted to disentangle the ecological effects of anthropogenic climate trends from those of climate regime shifts (Beaugrand 2012). Additionally, understanding of the importance of climate regime shifts relative to other ecosystem perturbations has developed differently in different regions, and regime shifts are seen as playing a more dominant ecological role in the North Pacific than they do in the North Atlantic. This difference may stem from differences in the relative importance of climate regime shifts and anthropogenic impacts in the two ocean basins. Four of the six leading modes of global sea surface temperature (SST) variability, explaining 30.1% of total variance, are centered in the Pacific, while only two of the six, explaining 8.1% of total variance, are centered in the Atlantic (Messié and Chavez 2011). Furthermore, North Atlantic ecosystems have often suffered persistent overfishing (Essington et al. 2006, Worm et al. 2009, Collie et al. 2013), which has had strong effects on community structure (e.g., Worm and Myers 2003, Choi et al. 2004, Frank et al. 2013). However, climate variability may also contribute to community change in overexploited ecosystems (Halliday and Pinhorn 2009, Beaugrand and Kirby 2010, Greene 2013), so a number of studies have attempted to identify the relative importance of overfishing and climate variability, among other drivers, in regulating community composition and structure in North Atlantic systems (e.g., Scotian Shelf, North Sea, Baltic Sea; Choi et al. 2005, Möllmann et al. 2009, Lindegren et al. 2012a,

Möllmann and Diekmann 2012). In contrast, while some areas of the North Pacific have been overfished (Harvey et al. 2006, Worm et al. 2009, Milazzo 2012), other areas, such as the eastern Bering Sea and northern Gulf of Alaska, have largely been free from overfishing (Litzow and Urban 2009, Milazzo 2012), and have been proposed as models of generally successful fisheries management (Witherell et al. 2000, Stram and Evans 2009, Worm et al. 2009). These areas are also strongly affected by leading global modes of internal climate variability (i.e., the El Niño-Southern Oscillation [ENSO], Pacific Decadal Oscillation [PDO] and North Pacific Gyre Oscillation [NPGO] patterns; Messié and Chavez 2011). Accordingly, a view of internal climate variability as the most important driver of community-level variability, especially across climate regime shifts in 1976/77 and 1988/89, has developed in this region, and studies of the ecological effects of internal climate variability have often failed to consider alternate hypotheses invoking fishing or other human activities, or climate trends independent of internal climate variability (e.g., Francis and Hare 1994, Mantua et al. 1997, Anderson and Piatt 1999, Hare and Mantua 2000, Beamish et al. 2004, Litzow 2006, Di Lorenzo et al. 2008, Kaeriyama et al. 2009, Möllmann and Diekmann 2012). Although studies focusing solely on internal climate variability were necessary for developing understanding of the ecological effects of climate regime shifts, studies that simultaneously consider alternate hypotheses are a necessary further step for understanding the relative importance of different external drivers in producing community-level variability (Choi et al. 2005). Understanding the potential impacts of low-frequency climate variability relative to other external forcing mechanisms is particularly important given the ongoing potential for disruptive climate regime shifts in the North Pacific (Zwolinski and Demer 2012, Hatch 2013, Litzow and Mueter 2014).

In this study we assess the ability of various drivers (internal climate variability, climate change independent of internal variability, and commercial fishing) to explain decadal-scale (1965-2008) biological variability across the Gulf of Alaska and Bering Sea. For our analysis we used updates to 36 biological time series first published in a seminal demonstration of coherent basin-scale biological variability, across multiple taxa and trophic levels, in the Northeast Pacific (Hare and Mantua 2000). Although the original study included biological time series from the southern Northeast Pacific (southern Gulf of Alaska and California Current ecosystems), these areas have suffered from dramatic anthropogenic disturbances in recent decades, especially the widespread loss of anadromous fish habitat (Nehlsen 1997), that would be difficult to account for in the statistical models that we employed. Therefore we restricted our analysis to the northern part of the Northeast Pacific

(Alaskan waters in the U.S. Exclusive Economic Zone) where habitat loss has been much less pervasive (Nehlsen 1997). The specific goals of our study were 1) to assess the ability of a comprehensive set of leading modes of internal climate variability to explain decadal-scale patterns of climatic variability within our study region; 2) to assess the ability of the same modes of internal climate variability to explain decadal-scale biological variability in the region; and 3) to compare the evidence for the internal climate modes, climate change independent of those modes, and commercial fishing (total biomass removals) as explanatory variables for observed biological variability. Although coherent basin-scale biological variability has been studied in the North Pacific for ~20 years (e.g., Francis and Hare 1994), this is, to our knowledge, the first study that has used statistical models to evaluate the relative evidence for these different drivers as the causative agents.

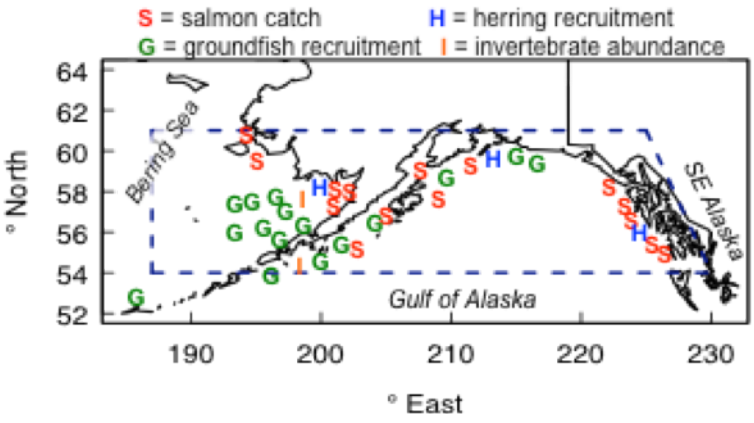

Fig. 1.1 Approximate locations for 36 biological time series included in analysis. Dashed line indicates spatial extent of SST and SLP data used in PCA of regional climate.

Materials and Methods

Data

We updated the biological time series first published by Hare and Mantua (2000) for the years 1965-2008; inherent lags in estimating many time series meant that too many values were missing for updates to more recent years. The update included 17 time series from the Bering Sea and 19 from the Gulf of Alaska (Fig. 1.1). These time series are dominated by parameters from commercially important fish populations, including time series of commercial salmon (*Oncorhynchus* spp.) catches (n = 15), log-transformed and lagged to year of ocean entry, and time series of groundfish (n = 16) and Pacific herring (*Clupea pallasii*, n = 3) recruitment estimates, log-transformed and lagged to cohort year. The data set also included two time series of invertebrate (Pandalid shrimp and jellyfish) abundance (complete list in Table 1.1). Details on time series updates are given in Appendix S1.1, and

complete time series descriptions and sources are in Table 1.S1. Justification for the inclusion of various time series, especially salmon catch data, is given by Hare et al. (1999) and Hare and Mantua (2000).

Table 1.1 Summary of the 36 biological time series used in analysis, ordered by common name. Complete details in Table 1.S1.
[a] Recruitment = estimated recruitment, log-transformed and lagged to cohort year; Catch = commercial catch, log-transformed and lagged to year of ocean entry; Abundance = survey-estimated biomass
[b] number of time series
[c] A = Aleutian Islands (part of Bering Sea ecosystem); B = Bering Sea; C = central Alaska (i.e., western Gulf of Alaska); G = Gulf of Alaska; W = western Alaska (Bering Sea with minor contribution from the Arctic); S = Southeast Alaska (part of Gulf of Alaska ecosystem).

Common name	Scientific name	Parameter[a]	*n*[b]	Region[c]
Alaska Plaice	*Pleuronectes quadrituberculatus*	Recruitment	1	B
arrowtooth flounder	*Atheresthes stomias*	Recruitment	2	B,G
Atka mackerel	*Pleurogrammus monopterygius*	Recruitment	1	A
Chinook salmon	*Oncorhynchus tsawytscha*	Catch	3	W,C,S
chum salmon	*Oncorhynchus keta*	Catch	3	W,C,S
coho salmon	*Oncorhynchus kisutch*	Catch	3	W,C,S
flathead sole	*Hippoglossoides elassodon*	Recruitment	1	B
Greenland turbot	*Reinhardtius hippoglossoides*	Recruitment	1	B
jellyfish	Scyphozoa	Abundance	1	B
Pacific cod	*Gadus macrocephalus*	Recruitment	2	B,G
Pacific halibut	*Hippoglossus stenolepis*	Recruitment	1	G
Pacific herring	*Clupea pallasii*	Recruitment	3	B,G,S
Pacific Ocean perch	*Sebastes alutus*	Recruitment	2	A,G
pink salmon	*Oncorhynchus gorbuscha*	Catch	3	W,C,S
rock sole	*Lepidopsetta* spp.	Recruitment	1	B
sablefish	*Anoplopoma fimbria*	Recruitment	1	G
shrimp	Pandalidae	Abundance	1	G
sockeye salmon	*Oncorhynchus nerka*	Catch	3	W,C,S
walleye pollock	*Theragra chalcogramma*	Recruitment	2	B,G
yellowfin sole	*Limanda aspera*	Recruitment	1	B

Ecologists seeking to capture all of the recognized leading modes of internal climate variability operating in a particular ocean basin are confronted with a diverse array of proposed indices. We sought a non-redundant set of indices, describing the imprint of fundamental climate processes, that could capture the full range of internal climate variability that might be expected to be ecologically important in our study region. The resulting set included the first and second modes of detrended North Pacific SST/sea surface height fields (Pacific Decadal Oscillation [PDO] and North Pacific Gyre Oscillation [NPGO]), the first and second modes of Northern Hemisphere sea level pressure (SLP) fields (the Arctic Oscillation [AO, also known

as the Northern Annular Mode] and Pacific-North American Pattern [PNA]), and the North Pacific Index (NPI), the average of regional SLP that captures variability in the Aleutian Low. This set includes the most important climate indices implicated by studies of climate regime shifts in the North Pacific (Minobe 1999, Overland et al. 1999, Mantua and Hare 2002, Schwing et al. 2003, Overland and Wang 2005, Di Lorenzo et al. 2008, Messié and Chavez 2011). As a measure of El Niño-Southern Oscillation (ENSO) activity we included annual mean values of the Multivariate ENSO Index (MEI), lagged one year to account for delay in propagation of the tropical ENSO signal to our study region (sources for climate indices in Table 1.S2). Leading modes for Northern Hemisphere SLP and detrended North Pacific SST show the most coherent variability in the winter season, due to a decadal-scale intensification in winter atmospheric circulation over the North Pacific, and a seasonal peak in midlatitude response to tropical SST forcing during the winter (Yeh et al. 2011). We therefore used winter values for the internal climate modes in our analysis, with the months used conforming to convention for each index (NDJFM for the PDO and NPGO, JFM for the AO and PNA, DJF for the NPI).

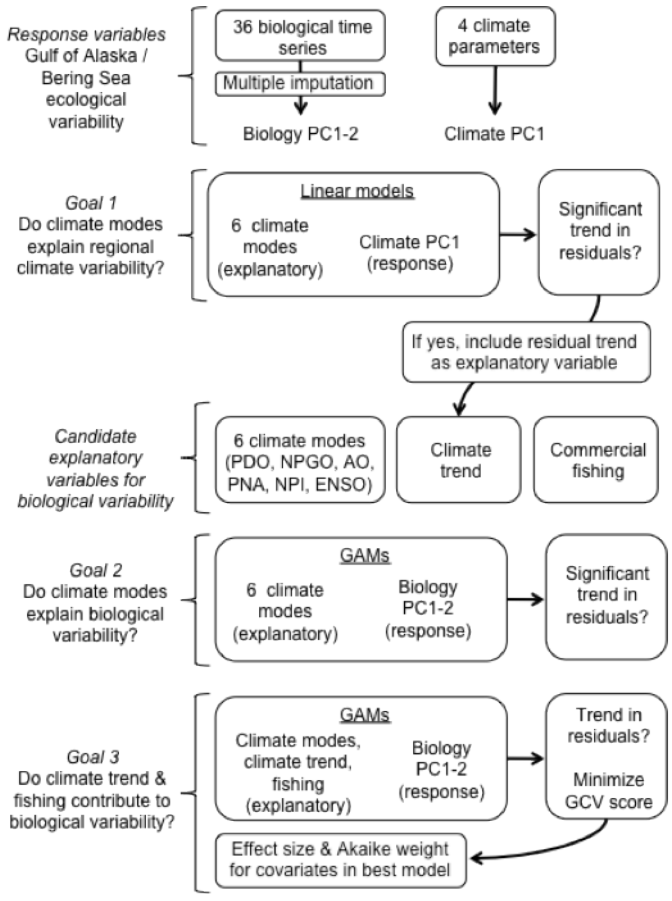

Fig. 1.2 Schematic of analytical steps used in the study.

To measure regional-scale climate variability we used ecologically important parameters that were available at the time scale of our analysis. These parameters included SST and SLP values for the combined Gulf of Alaska and Bering Sea, Gulf of Alaska freshwater discharge and Bering Sea ice cover (sources in Table 1.S2). Mean SST and SLP were calculated for a polygon with corners at 61°N 173°W, 61°N 135°W, 54°N 130°W and 54°N 173°W (Fig. 1.1), and winter (NDJFM) values were used to achieve a seasonal match with the leading climate modes. Finally, as a measure of commercial fishing effects we used a time series constructed from best available estimates of

total biomass removals (retained catch and, where available, discards) for domestic (U.S.) and international fleets (Litzow and Urban 2009).

Analysis

Our analysis sought to derive the best explanations for observed patterns of decadal-scale climatic and biological variability in our study region, using a suite of potential covariates (drivers). A multi-step analytical approach was required to summarize multivariate variability in the response variables and to account for temporal autocorrelation in both drivers and response variables, and for multicollinearity in drivers. We summarize our analysis around the three study goals, and provide a schematic diagram outlining our analytical steps in Fig. 1.2.

We began analysis by using principal components analysis (PCA) to summarize variability in response variables (regional climate and biology). We were interested in the most important axes of ecological variability, so analysis was restricted to PC1 for the regional climate variables, and PC1 and 2 for biology variables. The "broken-stick" and bootstrapped-λ approaches of Jackson (1993) were used to confirm that these PCs were interpretable. Because missing values for biology time series (8.6% of time series values) were non-randomly distributed (i.e., clustered at the beginning and ending of time series, Table 1.S1), annual PC scores calculated from the incomplete data set would likely be biased. In order to obtain unbiased PC scores and to estimate the uncertainty associated with estimating missing values, we used a multiple imputation approach to fill in missing values prior to computing PC scores for each imputed dataset. We first calculated eigenvectors (loadings) and eigenvalues from a correlation matrix of the incomplete time series, using a singular value decomposition with function "svd" in the computer language R (R Development Core Team 2010). We then estimated the mean and distribution of each missing value using multiple imputation implemented with Bayesian linear regression techniques in the R package "mice" (Van Buuren and Oudshoorn 1999), and randomly drew 100 sets of imputed time series from the resulting distributions. Finally, we estimated annual PC scores for each imputed dataset by applying the PCA loadings to the complete time series, and then computed the mean and standard deviation (SD) for the annual PC scores across all 100 imputed values. The SD of the annual scores allowed us to assess the uncertainty associated with estimating missing values; if the SD for any year was greater than the mean

absolute value for the corresponding PC score across all years of the time series, we judged that too much uncertainty had been introduced by estimating missing values, and these estimates were excluded from further analysis.

Goal 1: Assess the ability of large-scale climate modes to explain regional climatic variability

We tested for the ability of the large-scale climate modes to explain observed patterns of regional climate variability using multiple linear regression (Fig. 1.2). The use of linear models is consistent with the linear methods (EOFs/PCA) used to derive the modes from anomaly fields of fundamental climate parameters. This analysis was conducted both with the full model (i.e., invoking the PDO, NPGO, AO, PNA, NPI and MEI) in order to maximize the proportion of variance explained, as well as with the best model, as determined by Akaike's Information Criterion adjusted for small sample size (AICc). Residuals from regression models were tested for significant trends, which would indicate both that the model violated the assumption of independent residuals, and that the model failed to explain a coherent pattern of regional climate variability. To calculate appropriate *P*–values for residual trends in the presence of potential serial autocorrelation, we employed a generalized least-squares (GLS) approach with first-order autocorrelated residuals and year as a linear predictor variable, using the package "nlme" in R (Pinheiro and Bates 2000). Multicollinearity was present among the large-scale climate modes (Table 1.S3), so we did not calculate *P*-values for individual covariates (Graham 2003).

Goal 2) Assess the ability of the large-scale climate modes to explain regional biological variability

Biological communities are expected to show non-linear responses to persistent external forcing (Smith et al. 2009), so our analysis of climate-biology covariation used generalized additive models (GAMs), which allow nonlinear forcing-response relationships to be fit (Fig. 1.2). This analysis was conducted with the R package "mgcv" (Wood 2006). We restricted the degree of smoothing in the GAM analysis by limiting parameter effective degrees of freedom to ≤ 3, which corresponds to a biologically realistic set of possible forcing-response relationships (linear, dome-shaped, sigmoidal), and we also limited the number of total covariates in all GAMs to five to reduce the chance of over-fitting models. We smoothed the climate modes (except the MEI) with a 3-year running mean, centered on the year of interest, for analysis of biological variability. Our reasoning was two-fold. First, we expected

biological systems to respond strongly to changes in mean climate state, but to be more resilient to stochastic (interannual) variability around that mean. Second, we expected the early life-history processes that dominate the time series in our study (i.e., recruitment and juvenile survival) to be most sensitive to processes occurring at lags of -1 (e.g., adult feeding, migration and spawning behavior), 0 (e.g., advection of eggs and larvae) and 1 (e.g., juvenile survival) years. The inclusion of climate data at lag 1 year through smoothing is justified by the fact that most of the biological time series in our study had also been lagged between 1 and 8 years in order to reflect year class strength (for groundfish and herring) or cohort strength at ocean entry (for salmon).

We report results for the five best models that could be constructed for each biology PC when invoking only the large-scale climate modes as explanatory variables. We recognize that selection from the full set of models is not typically recommended (Burnham and Anderson 2002), but in this case there is strong support for a role of each individual parameter in structuring ecological variability (e.g., Minobe 1999, Overland et al. 1999, Mantua and Hare 2002, Overland and Wang 2005, Di Lorenzo et al. 2008, Schwing et al. 2010), so our goal was to evaluate the ability of the best models invoking these modes to explain biological variability; hence model selection from a global set of covariates was judged to be appropriate in this instance. Model selection was conducted by minimizing the generalized cross validation (GCV) score, which rewards model parsimony and predictive power. We then tested the best five models for each biology PC score for significant linear trends in residuals, again using a GLS approach.

Goal 3) Compare the evidence for internal climate modes, climate change independent of those modes, and commercial fishing as explanatory variables for biological variability

Finally, we tested the ability of different sets of candidate forcing variables (large-scale climate modes alone or the climate modes along with commercial catch and the regional climate trend independent of the climate modes) to explain leading axes of community variability, as summarized by biology PC1 and PC2 (Fig. 1.2). The regional climate trend was defined as the residual time series from the regression of regional climate PC1 on the full set of climate modes (details in *Results*). We expected commercial catch to have a lagged effect on community variability, and an initial round of model selection to evaluate the effect of catch at lag 1-3 years showed consistently strongest effects (for both PC series) at lag 3. Catch data were accordingly lagged 3 years for analysis. We present results for the five best models that could be constructed for each biology PC score, test the residuals for significant

trends with GLS, and compare support for these models (in terms of GCV scores) with the five best models for each PC score that could be constructed only from the climate modes.

Evaluating the support for individual covariates as drivers of biological variability could not rely on *P*-values, as multicollinearity was also present in the set of external variables for this analysis (Table 1.S4). We therefore evaluated the importance of individual parameters from the best model for each PC in terms of effect size and evidence for being included in the true model. Effect size was calculated as the proportion of deviance uniquely explained by each explanatory variable. For each biology PC, we fit a set of reduced models derived from the best GAM, removing each forcing variable in turn while maintaining the smoothing parameters for the remaining variables equal to the smoothing parameters from the full model. If **F** = the full model, **N** = the null model (i.e., $y = \bar{y} + \varepsilon$, with 0% of deviance explained), and **X** = the reduced model, with variable *x* removed, then the proportion of deviance uniquely explained by *x* can be calculated as: (deviance(**X**) – deviance(**F**)) / deviance(**N**) (S. Wood, public comm., accessed 2 July 2011, R Project / R Help, r.789695.n4.nabble.com/variance-explained-by-each-term-in-a-GAM-td836513.html). We also evaluated the evidence supporting individual parameters by summing Akaike weights (*w*) over the set of models including a given parameter (Burnham and Anderson 2002).

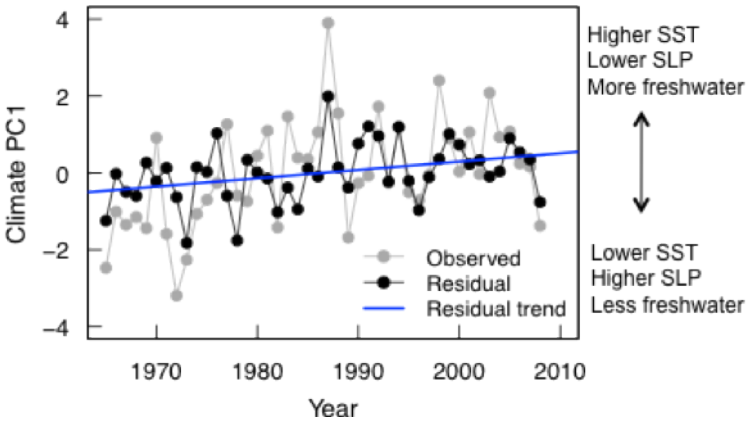

Fig. 1.3 Inability of large-scale climate modes to explain regional climate variability: observed values of climate PC1, and residual values from linear model invoking full set of climate modes (PDO, NPGO, AO, PNA, NPI, MEI lag1). Significant linear trend in model residuals (P = 0.03) indicates that the model fails to capture a directional trend in regional climate, and therefore violates the assumption of independent residuals.

Results

Goal 1

Climate PC1 explained 48% of variability in the regional climate parameters and showed strongest loadings on SST (0.59), SLP (-0.59) and Gulf of Alaska freshwater discharge

(0.53), with a weaker loading on Bering Sea ice cover (-0.17). Climate PC1 showed a significant linear trend during 1965-2008 (GLS, $P = 0.02$), indicating increasing winter SST, increasing freshwater input, and decreasing winter SLP during that time. This trend could not be completely explained by the modes of internal climate variability; residuals from the linear model invoking the full set of climate modes (PDO, NPGO, AO, PNA, NPI, MEI) also showed a significant linear trend (GLS, $P = 0.03$, Fig. 1.3). This trend indicated that the model failed to meet assumptions of independent residuals. The best linear model that could be constructed from the climate modes alone (invoking the PDO and NPI) showed a similar trend in residuals (GLS, $P = 0.03$). Since the residual trend from the full model captures a pattern of coherent climate variability that is by definition independent of the climate modes, we used the residuals from the full model, smoothed with a 3-year running mean, as an additional candidate covariate in models of variability in biology PC series. We refer to this additional covariate as the "climate trend"; time series of all candidate covariates for models of biological variability are plotted in Fig. 1.S1.

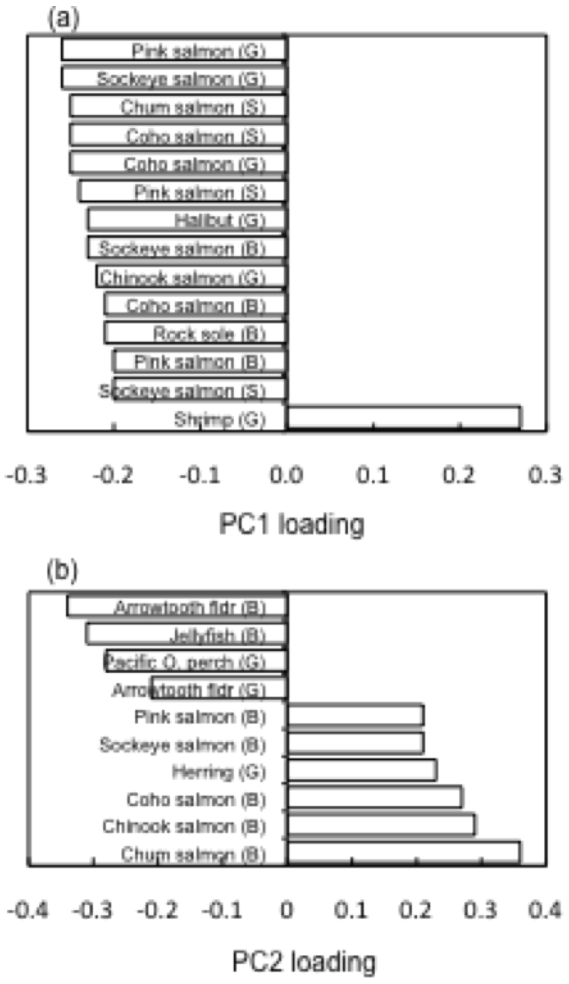

Fig. 1.4 Strongest loadings (absolute value ≥ 0.2) for (a) biology PC1 and (b) biology PC2. Complete loadings are presented in Table S5. G = Gulf of Alaska, S = Southeast Alaska (part of the Gulf of Alaska ecosystem), B = Bering Sea.

Goal 2

Biology PC1 explained 30.6% of total variance, and showed strong loadings (absolute value ≥ 0.2) on fourteen time series. Eleven salmon time series, from across the study area, showed negative loadings, as did Gulf of Alaska halibut and Bering Sea rock sole; Gulf of Alaska shrimp showed a positive loading (Fig. 1.4a). Biology PC2 explained 12.4% of total variance, and showed strong loadings on ten time series: negative loadings by Bering Sea

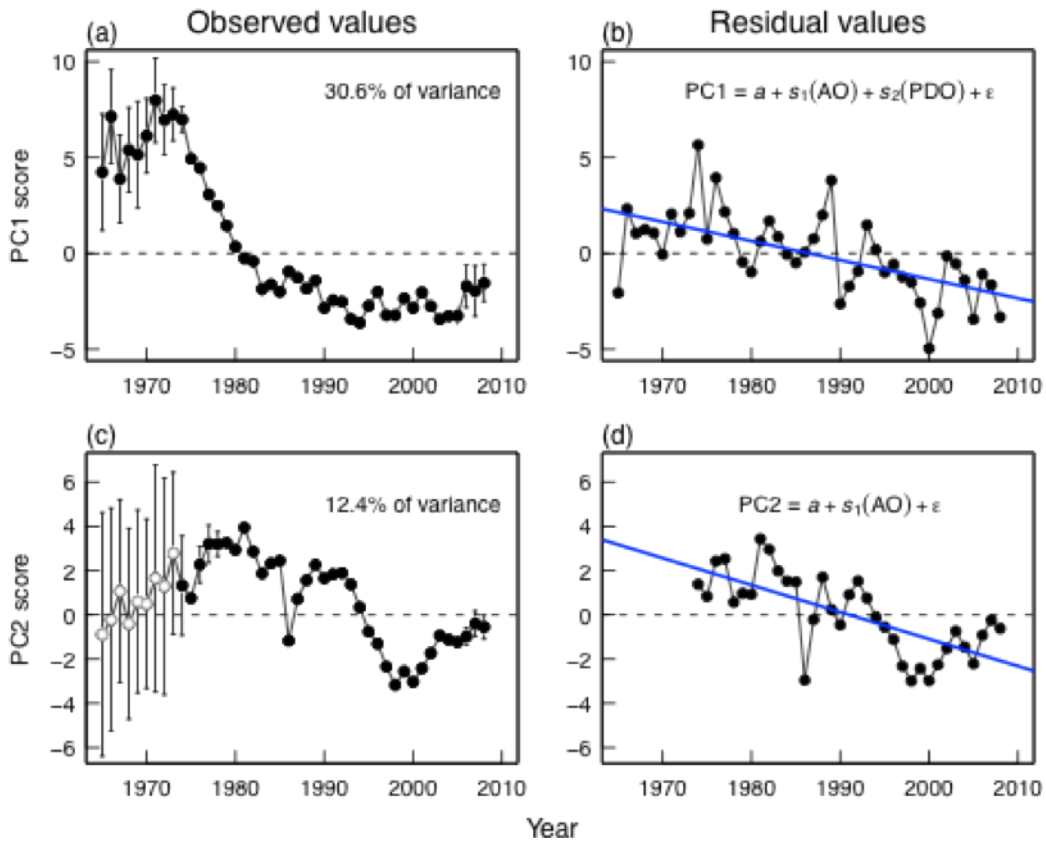

Fig. 1.5 Inability of internal climate variability to explain regional biological variability: time series of observed scores for biology PC1 and PC2 (a, c), and residual scores from best GAMs that could be constructed from internal climate modes alone (b, d). Observed values are mean ± 2 SD from the final 100 imputations used to estimate missing values in individual biology time series (see *Methods* for details). Years without error bars contained no missing values. Open circles in (c) indicate years where SD of estimated PC2 was greater than the absolute value of mean estimated scores across the time series; these years were not used in subsequent analysis. Plotted residuals from best GAMs invoking only internal climate modes (b, d) show linear trends (heavy lines) that were significant in both cases (PC1: $P = 0.001$; PC2: $P = 0.002$), indicating that the models failed to explain directional trends in community variability, and therefore violated the assumption of independent residuals.

jellyfish and arrowtooth flounder and Gulf of Alaska Pacific Ocean perch and arrowtooth flounder; and positive loadings by all five species of Bering Sea salmon and Prince William Sound herring (Fig. 1.4b; complete PCA loadings in Table 1.S5).

Our biology PC1 and 2 were well correlated, for the period of overlap, with PC1 and 2 from the biology time series for the entire northeast Pacific originally published by Hare and Mantua (2000; PC1: $r = 0.96$, PC2: $r = 0.62$). The time series of biology PC1 scores captures the well-documented transition (Anderson and Piatt 1999, Hare and Mantua 2000), during the 1970s and 1980s, from a crustacean-abundant state to a groundfish- and salmon-abundant state (Fig. 1.5a). Estimates for biology PC2 scores in 1965-1973 had SD values > the mean absolute value of PC2 scores across the time series, so these years were excluded from

Table 1.2 Model selection results for biology PC1 and PC2; best five GAMs for each PC constructed from the climate modes only, or from the climate modes, residual climate change independent of those modes and commercial catch. Bold type indicates models with significant linear trend in residuals
[a] AO = Arctic Oscillation, CATCH = total commercial catch lagged 3 years, CT = residual climate trend, MEI = multivariate ENSO index lagged 1 year, NPGO = North Pacific Gyre Oscillation, NPI = North Pacific Index, PDO = Pacific Decadal Oscillation, PNA = Pacific-North America Pattern
[b] Generalized Cross-Validation score

Response variable	Candidate covariates	Model[a]	Residual trend *P*	GCV[b]	Δ-GCV	Dev. expl.
PC1	Climate modes only	$a + s_1(\text{AO}) + s_2(\text{PDO}) + \varepsilon$	**0.001**	5.20	1.83	69.1%
		$a + s_1(\text{AO}) + s_2(\text{PDO}) + s_3(\text{PNA}) + \varepsilon$	**0.001**	5.24	1.87	70.3%
		$a + s_1(\text{AO}) + s_2(\text{NPGO}) + s_3(\text{PDO}) + \varepsilon$	**0.003**	5.31	1.94	70.4%
		$a + s_1(\text{AO}) + s_2(\text{NPI}) + s_3(\text{PDO}) + \varepsilon$	**0.004**	5.33	1.96	70.2%
		$a + s_1(\text{AO}) + s_2(\text{NPGO}) + s_3(\text{PDO}) + s_4(\text{PNA}) + \varepsilon$	**0.002**	5.41	2.04	71.1%
PC1	Climate modes, climate trend, commercial catch	$a + s_1(\text{CATCH}) + s_2(\text{CT}) + s_3(\text{MEI}) + s_4(\text{NPI}) + s_5(\text{PDO}) + \varepsilon$	0.16	3.37	0.00	86.3%
		$a + s_1(\text{CATCH}) + s_2(\text{CT}) + s_3(\text{MEI}) + s_4(\text{NPI}) + s_5(\text{PNA}) + \varepsilon$	0.20	3.50	0.13	87.0%
		$a + s_1(\text{CATCH}) + s_2(\text{CT}) + s_3(\text{NPI}) + s_4(\text{PDO}) + s_5(\text{PNA}) + \varepsilon$	0.09	3.63	0.26	85.5%
		$a + s_1(\text{AO}) + s_2(\text{CATCH}) + s_3(\text{CT}) + s_4(\text{MEI}) + s_5(\text{NPI}) + \varepsilon$	0.10	3.66	0.29	85.1%
		$a + s_1(\text{AO}) + s_2(\text{CATCH}) + s_3(\text{CT}) + s_4(\text{NPI}) + s_5(\text{PDO}) + \varepsilon$	**0.048**	3.66	0.29	83.7%
PC2	Climate modes only	$a + s_1(\text{AO}) + \varepsilon$	**0.01**	3.66	2.44	26.7%
		$a + s_1(\text{AO}) + s_2(\text{NPGO}) + \varepsilon$	**0.01**	3.72	2.50	32.1%
		$a + s_1(\text{AO}) + s_2(\text{MEI}) + \varepsilon$	**0.01**	3.87	2.65	27.1%
		$a + s_1(\text{AO}) + s_2(\text{PDO}) + \varepsilon$	**0.01**	3.88	2.66	27.1%
		$a + s_1(\text{AO}) + s_2(\text{PNA}) + \varepsilon$	**0.01**	3.90	2.68	26.6%
PC2	Climate modes, climate trend, commercial catch	$a + s_1(\text{AO}) + s_2(\text{CATCH}) + s_3(\text{CT}) + s_4(\text{NPGO}) + s_5(\text{PNA}) + \varepsilon$	0.18	1.22	0.00	84.5%
		$a + s_1(\text{CATCH}) + s_2(\text{CT}) + s_3(\text{NPGO}) + s_4(\text{PNA}) + \varepsilon$	0.20	1.23	0.01	84.1%
		$a + s_1(\text{CATCH}) + s_2(\text{CT}) + s_3(\text{MEI}) + s_4(\text{NPGO}) + s_5(\text{PNA}) + \varepsilon$	0.37	1.26	0.04	84.6%
		$a + s_1(\text{CATCH}) + s_2(\text{CT}) + s_3(\text{NPGO}) + s_4(\text{NP1}) + s_5(\text{PNA}) + \varepsilon$	0.23	1.29	0.07	85.4%
		$a + s_1(\text{CATCH}) + s_2(\text{CT}) + s_3(\text{NPGO}) + s_4(\text{PDO}) + s_5(\text{PNA}) + \varepsilon$	0.21	1.32	0.10	84.1%

analysis of factors forcing PC2 variability. The remainder of the time series was associated with a transition, in the 1990s, from abundant Bering Sea salmon (all five spp.) and Prince William Sound herring to abundant jellyfish and arrowtooth flounder in the Bering Sea, and Pacific Ocean perch and arrowtooth flounder in the Gulf of Alaska (Fig. 1.5c).

The best statistical models of biological variability that could be constructed from the climate modes alone invoked the AO and PDO for biology PC1, and the AO for biology PC2. However, both of these models showed significant linear trends in residuals (GLS; $P \leq 0.01$; Fig. 1.5b,d), indicating that they failed to capture directional trends in the leading modes of biological variability, thereby violating the assumption of independent residuals. Similar significant trends in residuals were shown for all five of the best models that could be constructed for each PC series from the climate modes alone (Table 1.2).

Goal 3

When the full set of candidate forcing mechanisms (internal climate modes, the climate trend and commercial catch) was employed, four of the five best models for biology PC1, and all five of the best models for biology PC2, met the assumption of independent residuals (GLS, $P \geq 0.09$, Table 1.2). The best model for biology PC1 using the full set of candidate variables invoked commercial catch, the climate trend, the MEI, the NPI and the PDO, with the climate trend accounting for the highest proportion of unique deviance (Fig. 1.6a-e). Evidence across models also showed the climate trend to be the most likely of these five covariates to be included in the true model (Fig. 1.6f). The best model for biology PC2 that could be constructed from the full set of candidate parameters invoked the AO, commercial catch, the climate trend, the NPGO and the PNA as explanatory variables, with commercial catch explaining 1.8 times the unique deviance of the covariate with the next-greatest effect size (Fig. 1.6g-k). Akaike weights showed strongest support for commercial catch and the NPGO as explanatory variables for biology PC2 ($w > 0.99$, Fig. 1.6l).

Discussion

Understanding statistical relationships between environmental factors and marine populations presents a suite of methodological difficulties (Daskalov et al. 2003), and the seminal studies of climate regime shift effects on North Pacific ecosystems often did not test statistical hypotheses of climate-biology covariation (e.g., Mantua et al. 1997, Anderson and Piatt

1999). Advances in statistics and computing over the last decade have made this problem more tractable, and the non-parametric regression (i.e., GAM) approach that we use here is now commonly employed to make inferences about the factors producing non-linear behavior in biological time series (Daskalov et al. 2003, Ciannelli et al. 2004, Litzow and Ciannelli 2007, Brodeur et al. 2008, Stige et al. 2010, Mueter et al. 2011, Siddon et al. 2011, Smart et al. 2012). We show conclusively that leading modes of internal climate variability in the North Pacific are by themselves inadequate to explain leading axes of climatic (Fig. 1.3) and biological (Fig. 1.5, Table 1.2) variability in the Gulf of Alaska and Bering Sea ecosystems over a 44-year period, as indicated by significant trends in model residuals. However, when the set of candidate covariates was enlarged to include the residual trend in climate PC1 and a time series of total commercial fishery biomass removals, best GAMs for biology PC1 and PC2 met assumptions of independent residuals and provided high degrees of explanatory power (Fig. 1.6, Table 1.2). These results suggest that the view of decadal-scale ecological variability in this study region as being dominated by internal climate variability (e.g., Hare and Mantua 2000, Benson and Trites 2002, Möllmann and Diekmann 2012) should be expanded to include the effects, at least, of commercial fishing and climate change unrelated to internal variability. Additionally, linear effects of the climate trend (Fig. 1.6b) and commercial catch (Fig. 1.6h) on biology PC1 and PC2, respectively, also suggest the importance of incremental ecosystem forcing on biological change in the region, which argues against an understanding of regional ecosystem dynamics based entirely on abrupt shifts between quasi-steady states (Lees et al. 2006, Spencer et al. 2012, Litzow and Mueter 2014).

Understanding the operation of marine ecosystems at large spatial scales requires the use of observational data sets that provide weak inference (Platt 1964), are open to competing interpretations (e.g., Frank et al. 2013, Greene 2013), and often suggest statistical forcing-response relationships that quickly break down as further observational data are collected (Myers 1998). Given these considerations, understanding of mechanistic relationships underlying modeling results is critical. A large body of research demonstrates specific mechanisms by which salmon populations in our study region respond to variability in SST, air temperature, precipitation, advection, large-scale air circulation patterns and freshwater discharge (Welch et al. 1998, Willette et al. 2001, Mueter et al. 2002, Taylor 2008, Wells et al. 2008, Martinson et al. 2009, Abdul-Aziz et al. 2011); groundfish populations respond to variability in SST, bottom temperature, SLP, advection and wind direction (Wilderbuer et al. 2002, Ciannelli et al. 2005, Mueter and Litzow 2008, Mueter et al. 2009, Mueter et al. 2011);

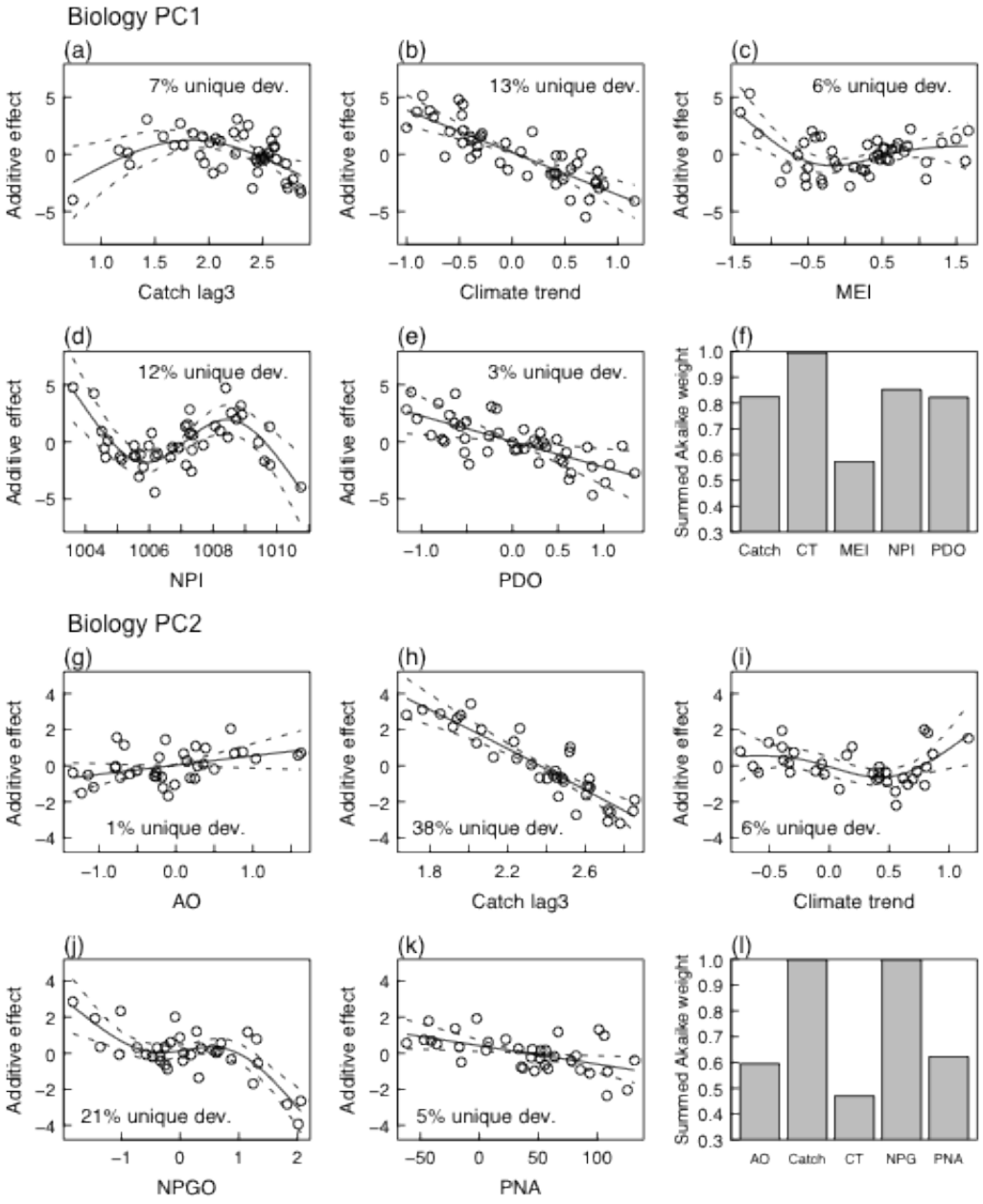

Figure 1.6 External forcing of leading axes of community-level biological variability. Partial residual plots from best GAM for biology PC1 (a-e) and biology PC2 (g-k) that could be constructed when invoking the full set of forcing variables (internal climate modes, residual climate trend and commercial catch). Solid lines indicate predicted effects with other variables held constant at their mean, dashed lines = 95% CI. Text in each panel indicates effect size in model (proportion of deviance uniquely explained by each covariate). Akaike weights for each variable included in best model for biology PC1 (f) and biology PC2 (l), summed across the global set of candidate models for each PC. Catch = commercial catch, CT = climate trend.

herring populations respond to variability in ice cover and SST (Tojo et al. 2007, Deriso et al. 2008); jellyfish populations respond to variability in SST, ice cover, advection and wind mixing (Brodeur et al. 2008); and shrimp populations respond to variability in SST and bottom temperature (Litzow and Ciannelli 2007, Mueter and Litzow 2008). The coherent

large-scale patterns of climate variability that are summarized by the climate modes in our study affect individual populations through simultaneous change to the set of climate parameters that are important for regulating particular populations in particular locations (Mantua and Hare 2002, Di Lorenzo et al. 2008). Simultaneous regional change in SST, SLP and freshwater discharge that is independent of those climate modes (Fig. 1.3), could plausibly be expected to regulate the populations loading heavily on biology PC1 in a similar fashion. Coherent community-level variability in turn arises both from covariation among populations exposed to large-scale patterns of climate variability (Wilderbuer et al. 2002, Mueter et al. 2007) and from climate regulation of species interactions, such as predation and competition (Litzow and Ciannelli 2007, Poloczanska et al. 2008). However, emergent properties, feedbacks, synergistic effects and other behaviors of complex systems preclude a simple understanding of the factors regulating community-level variability from the sum of population-level responses (Drake 1991, Scheffer et al. 2001). Additionally, observational studies are unable to distinguish the factors maintaining a community in its current state from the factors that initially produced the observed state (Drake 1991), or to distinguish, *a priori*, persistent community states from transients (Frank et al. 2011). These considerations make a mechanistic understanding of the apparent relationship between the residual climate trend and biology PC1 (Fig. 1.6b,f) beyond the scale of this study. Additionally, our results support the view that internal climate variability is an important, though not sufficient, explanation for community variability summarized by biology PC1. The NPI and PDO indices track the atmospheric and oceanic imprints, respectively, of a single pattern of large-scale climate variability (Minobe 1999, Mantua and Hare 2002, Schwing et al. 2003), which is mechanistically related to ENSO variability (Newman et al. 2003). The combined effect size of these indices (Fig. 1.6c-e) supports the view that low-frequency internal climate variability remains critical for understanding large-scale ecological variability in the North Pacific, especially with recent interest in indications of a possible switch to persistently PDO-negative conditions in the mid-late 2000s (Cai and van Rensch 2012, Zwolinski and Demer 2012, Hatch 2013, Litzow and Mueter 2014).

At the onset of industrial-scale fishing in the northern Gulf of Alaska and eastern Bering Sea, in the 1960s and 1970s, several taxa (e.g., various crabs and Pandalid shrimp, Pacific Ocean perch, yellowfin sole) were severely overfished (Orensanz et al. 1998, Litzow and Urban 2009). However, fisheries management in the region matured and became much more conservative in the 1980s, and these systems have been free of egregious overfishing for decades, as indicated by ecosystem models, stock assessments and fisheries-independent

surveys (Worm et al. 2009), the number of stocks under rebuilding plans relative to other ecosystems under U.S. jurisdiction (Milazzo 2012), and stability in catches at decadal time scales (Litzow and Urban 2009). Our finding that commercial catch plays a leading role in regulating biology PC2 (Fig. 1.6h,l) therefore occurs in the absence of ongoing overfishing. Inference of a relationship between commercial catch and biology PC2 variability is supported by the exploitation history of taxa loading heavily on this axis of variability; the four populations showing loadings ≤ -0.2, associated with an increasing trend, are either not subject to a directed fishery (Bering Sea jellyfish, Bering Sea and Gulf of Alaska arrowtooth flounder) or have been recovering from overfishing during the 1960s (Gulf of Alaska Pacific Ocean perch, Litzow and Urban 2009). Commercial fishing has the potential to change community composition (Harvey et al. 2006) and the linear relationship between total catch and biology PC2 scores (Fig. 1.6h) is consistent with a direct, ongoing influence of fishing pressure on community structure. In particular, awareness has been growing for several years that increases in arrowtooth flounder populations in the Gulf of Alaska and Bering Sea may reflect the lower exploitation pressure on this species relative to other groundfish, with a positive feedback created by increased arrowtooth flounder predation on other groundfishes (Bailey 2000, Zador et al. 2011, Bailey et al. 2012).

The residual trend in regional climate PC1 (Fig. 1.3) reflects patterns of rising SST, decreasing SLP and rising freshwater input that are not explained by linear relationships with the leading modes of internal climate variability in the North Pacific (PDO, NPGO, AO, PNA, NPI, ENSO). We caution that our regional-scale analysis may have obscured variability in physical parameters within the Gulf of Alaska or Bering Sea. Basin-scale increases in North Pacific SST over recent decades, and decreases in SLP, have been attributed to anthropogenic forcing (Gillett et al. 2003, Hegerl et al. 2007, Gillett and Stott 2009). Additionally, rapid increases in Gulf of Alaska freshwater input are due to glacier melting, which has not been attributed to any particular cause, but is expected to continue under anthropogenic warming (Arendt et al. 2002, Meier et al. 2003). Therefore, the residual climate trend in our study plausibly reflects the regional effects of anthropogenic climate change; however, we caution that attribution of the causes of this climate trend is beyond the scope of our study. General circulation model experiments are increasingly attributing the causes of observed climate variability at regional scales (Stott et al. 2010, Christidis et al. 2012); such a regional-scale attribution study would be needed to allow our results to be more firmly interpreted as a response to anthropogenic forcing. Additionally, while proxy studies show that the modes of large-scale internal climate variability in our study existed prior to the

accumulation of anthropogenic greenhouse gasses (Gedalof et al. 2002), variability in these modes is to some degree now affected by anthropogenic forcing (Morgenstern et al. 2010, Bonfils and Santer 2011). Therefore, just as the residual climate trend in our study cannot be formally attributed to anthropogenic forcing, the climate modes cannot be treated as tracking purely natural climate variability. The distinction between ecological effects of natural and anthropogenic climate change cannot therefore be made from our analysis, and we simply interpret our results as demonstrating the regional ecological importance of observed climate change that is independent of the leading climate modes. In summary, modes of internal climate variability remain important for understanding decadal-scale, basin-scale marine ecosystem variability, but a view of these modes as the most important factor in driving large-scale patterns of ecological variability may be obsolete, even in areas that are subject to strong internal climate variability and free of overfishing.

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Supporting Information

Appendix 1.S1 Detailed data methods

Sources and detailed descriptions for the Hare and Mantua (2000) biology time series are given in Table 1.S1. Five time series from our study region that appeared in the original paper (Eastern Bering Sea, Central Pacific and East Pacific zooplankton biomass; Gulf of Alaska shortspine thornyhead recruitment; Bering Sea Pacific Ocean Perch recruitment) have, to the best of our knowledge, not been updated since 1998, and were not included in our study.

The salmon catch data used in Hare and Mantua (2000) were combined estimates of commercial domestic, high-seas foreign, recreational and subsistence catches. However, these combined catch time series have not been maintained beyond the ocean entry year of 2000 (S. Hare, pers. comm.), so we used only commercial catch time series, for which more recent data were available. This choice is justified by the observation that adding recreational and subsistence catches has little influence on results obtained from commercial catches alone (Hare et al. 1999), and by the generally high correlations between our updated salmon catch time series and the original time series (mean $r = 0.95$). Lagging catches to year of ocean entry allows us to capture the strong effect of early marine survival on salmon populations (Hare et al. 1999, Mueter et al. 2002). While catch data can produce biased estimates of population trends (Branch et al. 2011), no fisheries-independent estimates of salmon population size are available at the spatial and temporal scales of interest to our study (Hare et al. 1999). However, there are several reasons to expect that commercial catches of salmon in our study are reasonable proxies for abundance. Spawning habitat for salmon in Alaska is relatively pristine (Nehlsen 1997), and salmon runs in our study area have been fully exploited and intensely managed throughout the time period of our study (Hare et al. 1999), so that catches are expected to primarily covary with abundance. A large number of studies have demonstrated coherent basin-scale variability in salmon runs that does not correlate with changes in management or market demand (reviewed in Hare et al. 1999). Finally, basin-scale patterns of variability demonstrated by catch data are confirmed by analysis of a subsample of runs for which fisheries-independent survival data are available (Mueter et al. 2002).

Occasionally, the current versions of time series did not extend as far back as the original time series in Hare and Mantua (2000). In seven instances, we were able to use

linear regression between the original and updated time series to estimate missing values for early years of the updated versions (mean R^2 = 0.92). Eighteen time series in our study are recruitment estimates from age-structured assessment models of commercially exploited fish stocks (Table 1.S1). The most recent estimates from these time series are often poorly supported by empirical data, and may represent either median values or estimates from poorly resolved stock-recruit relationships. Such estimates tend to assume a continuation of recent environmental conditions, and result in dampened sensitivity of these time series to recent ecological change. We therefore excluded such estimates from our analysis, identifying them either from personal communication with assessment authors, caveats within assessment reports, or the appearance of inflated variance estimates around recruitment in the final years of a time series.

Our set of internal climate modes included the first two modes of winter Northern Hemisphere SLP, the Arctic Oscillation (AO) and Pacific-North American Pattern (PNA) (Wallace and Gutzler 1981, Thompson and Wallace 1998, Wallace 2000, Thompson and Wallace 2001); the first and second modes of detrended North Pacific SST and sea surface height fields, the Pacific Decadal Oscillation (PDO) and North Pacific Gyre Oscillation (NPGO) (Mantua et al. 1997, Bond et al. 2003, Di Lorenzo et al. 2008); and El Niño-Southern Oscillation (ENSO), as measured by the Multivariate ENSO Index (MEI) (Walker and Bliss 1932, Wolter and Timlin 2011). We used SLP EOF2 for the PNA, rather than the original grid-point definition of Wallace and Gutlzer (1981). We also included the North Pacific Index (NPI), the mean SLP over a large area of the North Pacific, which measures the intensity of the Aleutian Low (Trenberth 1990, Trenberth and Hurrell 1994). During our study period the NPI is largely redundant with the PDO and PNA (Table 1.S2), and it also apparently conflates natural and anthropogenic climate change, as it covers an area of SLP declines attributed to anthropogenic forcing in GCM experiments (Gillett et al. 2003). However, we included the NPI in analysis because of its importance in the North Pacific climate literature. The NPI is very similar to another measure of Aleutian Low variability, the Aleutian Low Pressure Index (ALPI); these two indices are correlated at r = -0.87 during 1965-2008, so we did not include the ALPI in analysis. Finally, Bering Sea ice cover values for 1965-1978 were acquired from Mueter and Litzow (2008), those for 1979-2008 from www.beringclimate.noaa.gov, with the two time series combined through linear regression.

Table 1.S1 Descriptions and sources for biology time series included in study.

Code	Name	Scientific name	Source	*n* (years)	Missing (imputed) years
BSJELLY	Eastern Bering Sea jellyfish biomass	Scyphozoa	www.access.afsc.noaa.gov/reem/ EcoWeb/EcoChaptDataMainFrame.htm	31	1965-1974, 1976-1978
EBSPOLL	Eastern Bering Sea pollock recruitment	*Theragra chalchogramma*	http://www.fakr.noaa.gov/npfmc/resources-publications/safe-reports.html	44	-
EBSCOD	Eastern Bering Sea Pacific cod recruitment	*Gadus macrocephalus*	http://www.fakr.noaa.gov/npfmc/resources-publications/safe-reports.html	35	1965-1973
EBSYFS	Eastern Bering Sea yellowfin sole recruitment	*Limanda aspera*	http://www.fakr.noaa.gov/npfmc/resources-publications/safe-reports.html	40	2005-2008
EBSTRBT	Eastern Bering Sea Greenland turbot recruitment	*Reinhardtius hippoglossoides*	http://www.fakr.noaa.gov/npfmc/resources-publications/safe-reports.html	39	1965-1969
EBSATF	Eastern Bering Sea arrowtooth flounder recruitment	*Atheresthes stomias*	http://www.fakr.noaa.gov/npfmc/resources-publications/safe-reports.html	34	1965-1974
EBSRSOLE	Eastern Bering Sea rock sole recruitment	*Lepidopsetta* spp.	http://www.fakr.noaa.gov/npfmc/resources-publications/safe-reports.html	35	1965-1970, 2006-2008
EBSFSOLE	Eastern Bering Sea flathead sole recruitment	*Hippoglossoides elassodon*	http://www.fakr.noaa.gov/npfmc/resources-publications/safe-reports.html	34	1965-1973, 2008
EBSAKPLA	Eastern Bering Sea Alaska Plaice recruitment	*Pleuronectes quadrituberculatus*	http://www.fakr.noaa.gov/npfmc/resources-publications/safe-reports.html	34	1965-1971, 2006-2008

Code	Name	Scientific name	Source	*n* (years)	Missing (imputed) years
EBSHERR	Eastern Bering Sea herring recruitment	*Clupea pallasii*	G. Buck, Alaska Dept. of Fish & Game, pers. comm.	34	1965-1972, 2007-2008
AIATKA	Aleutian Islands Atka mackerel recruitment	*Pleurogrammus monopterygius*	http://www.fakr.noaa.gov/npfmc/resources-publications/safe-reports.html	32	1965-1974, 2007-2008
AIPOP	Aleutian Islands Pacific Ocean perch recruitment	*Sebastes alutus*	http://www.fakr.noaa.gov/npfmc/resources-publications/safe-reports.html	31	1965-1973, 2005-2008
WAK_CH	Western Alaska Chinook salmon catch	*Oncorhynchus tsawytscha*	www.cf.adfg.state.ak.us	44	-
WAK_CM	Western Alaska chum salmon catch	*Oncorhynchus keta*	www.cf.adfg.state.ak.us	44	-
WAK_CO	Western Alaska coho salmon catch	*Oncorhynchus kisutch*	www.cf.adfg.state.ak.us	44	-
WAK_PI	Western Alaska pink salmon catch	*Oncorhynchus gorbuscha*	www.cf.adfg.state.ak.us	44	-
WAK_SO	Western Alaska sockeye salmon catch	*Oncorhynchus nerka*	www.cf.adfg.state.ak.us	44	-
GOASHR	Gulf of Alaska shrimp catch	Pandalidae	D. Urban, National Oceanic and Atmospheric Administration, pers. comm	37	1965-1971
GOASAB	Gulf of Alaska sablefish recruitment	*Anoplopoma fimbria*	http://www.fakr.noaa.gov/npfmc/resources-publications/safe-reports.html	44	-
GOAHAL	Gulf of Alaska halibut recruitment	*Hippoglossus stenolepis*	S. Hare, International Pacific Halibut Commission, pers. comm.	41	2006-2008

Code	Name	Scientific name	Source	*n* (years)	Missing (imputed) years
GOAPOP	Gulf of Alaska Pacific Ocean perch recruitment	*Sebastes alutus*	http://www.fakr.noaa.gov/npfmc/resources-publications/safe-reports.html	34	1965-1974
GOAPOLL	Gulf of Alaska walleye pollock recruitment	*Theragra chalchogramma*	http://www.fakr.noaa.gov/npfmc/resources-publications/safe-reports.html	44	-
GOACOD	Gulf of Alaska Pacific cod recruitment	*Gadus macrocephalus*	http://www.fakr.noaa.gov/npfmc/resources-publications/safe-reports.html	44	-
GOAATF	Gulf of Alaska arrowtooth flounder recruitment	*Atheresthes stomias*	http://www.fakr.noaa.gov/npfmc/resources-publications/safe-reports.html	44	-
PWSHERR	Prince William Sound herring recruitment	*Clupea pallasii*	S. Moffit, Alaska Dept. of Fish & Game, pers. comm.	40	1965-1968
SITHERR	Sitka herring recruitment	*Clupea pallasii*	S. Dressel, Alaska Dept. of Fish & Game, pers. comm.	41	1965-1967
CAK_CH	Central Alaska Chinook salmon catch	*Oncorhynchus tsawytscha*	www.cf.adfg.state.ak.us	44	-
CAK_CM	Central Alaska chum salmon catch	*Oncorhynchus keta*	www.cf.adfg.state.ak.us	44	-
CAK_CO	Central Alaska coho salmon catch	*Oncorhynchus kisutch*	www.cf.adfg.state.ak.us	44	-
CAK_PI	Central Alaska pink salmon catch	*Oncorhynchus gorbuscha*	www.cf.adfg.state.ak.us	44	-
CAK_SO	Central Alaska sockeye salmon catch	*Oncorhynchus nerka*	www.cf.adfg.state.ak.us	44	-

Code	Name	Scientific name	Source	*n* (years)	Missing (imputed) years
SAK_CH	Southeast Alaska Chinook salmon catch	*Oncorhynchus tsawytscha*	www.cf.adfg.state.ak.us	44	-
SAK_CM	Southeast Alaska chum salmon catch	*Oncorhynchus keta*	www.cf.adfg.state.ak.us	44	-
SAK_CO	Southeast Alaska coho salmon catch	*Oncorhynchus kisutch*	www.cf.adfg.state.ak.us	44	-
SAK_PI	Southeast Alaska pink salmon catch	*Oncorhynchus gorbuscha*	www.cf.adfg.state.ak.us	44	-
SAK_SO	Southeast Alaska sockeye salmon catch	*Oncorhynchus nerka*	www.cf.adfg.state.ak.us	44	-

Table 1.S2 Climate data used in analysis: indices of leading modes of large-scale internal climate variability and regional climate parameters.

Time series	**Source**
Large-scale climate modes	
Arctic Oscillation (AO)	www.jisao.washington.edu
Multivariate ENSO Index (MEI)	www.esrl.noaa.gov
North Pacific Gyre Oscillation Index (NPGO)	www.o3d.org/npgo
North Pacific Index (NPI)	www.climatedataguide.ucar.edu
Pacific Decadal Oscillation Index (PDO)	www.jisao.washington.edu
Pacific-North American Pattern (PNA)	www.jisao.washington.edu
Regional climate parameters	
Bering Sea Ice Cover Index	Mueter & Litzow 2008[a], www.beringclimate.noaa.gov
Gulf of Alaska freshwater input	T. Royer, Old Dominion University, pers. comm.
Sea level pressure (NCEP/NCAR reanalysis)	www.ersl.noaa.gov
Sea surface temperature (ERSSTv3.b)	www.ncdc.noaa.gov

[a] Mueter FJ, Litzow MA (2008) Sea ice retreat alters the biogeography of the Bering Sea continental shelf. *Ecological Applications,* **18**, 309-320.

Table 1.S3 Pairwise Pearson's correlation coefficients between indices of large-scale climate variability.

	PDO	NPGO	AO	PNA	NPI
PDO	1.00				
NPGO	0.03	1.00			
AO	-0.19	0.07	1.00		
PNA	0.49	0.06	0.07	1.00	
NPI	-0.66	-0.12	0.20	-0.77	1.00
MEI (lag1)	0.63	-0.21	-0.10	0.45	-0.37

Table 1.S4 Pairwise Pearson's correlation coefficients for candidate variables used to explain regional biological variability. PDO, NPGO, AO, PNA, NPI and regional climate trend were smoothed with 3-year running mean. Climate trend was defined with residuals from regression of climate PC1 on the full set of internal climate modes.

	PDO	NPGO	AO	PNA	NPI	MEI (lag1)	Climate trend
PDO	1.00						
NPGO	-0.04	1.00					
AO	-0.13	0.06	1.00				
PNA	0.70	0.08	0.05	1.00			
NPI	-0.83	-0.11	0.22	-0.77	1.00		
MEI (lag1)	0.49	-0.29	0.04	0.46	-0.29	1.00	
Climate trend	0.25	0.20	0.54	0.33	-0.22	0.17	1.00
Catch (lag3)	0.20	0.07	0.63	0.27	-0.21	0.18	0.60

Table 1.S5. Complete loadings for biology PC1 and PC2, sorted in decreasing order.

PC1		**PC2**	
Time series	**Loading**	**Time series**	**Loading**
GOASHR	0.26	WAK_CM	0.41
EBSTRBT	0.24	WAK_CH	0.34
EBSYFS	0.14	WAK_CO	0.28
GOAPOLL	0.13	PWSHERR	0.23
PWSHERR	0.11	WAK_SO	0.21
EBSAKPLA	0.11	EBSRSOLE	0.16
WAK_CH	0.09	CAK_CO	0.15
EBS_BLKI	0.06	WAK_PI	0.15
SAK_CH	0.05	EBSFSOLE	0.14
EBSPOLL	0.03	EBSHERR	0.13
EBSFSOLE	0.01	GOAPOLL	0.11
WAK_CM	-0.01	SAK_SO	0.10
AIATKA	-0.02	CAK_CH	0.09
EBSCOD	-0.03	GOACOD	0.09
EBSHERR	-0.04	GOASHR	0.08
GOASAB	-0.07	CAK_SO	0.08
BSJELLY	-0.09	EBSYFS	0.07
SITHERR	-0.11	EBSPOLL	0.07
GOACOD	-0.13	GOASAB	0.01
GOAPOP	-0.14	SITHERR	0.00
CAK_CM	-0.15	EBSCOD	0.00
GOAATF	-0.18	EBSTRBT	-0.01
EBSRSOLE	-0.19	CAK_PI	-0.02
SAK_SO	-0.20	SAK_PI	-0.04
WAK_PI	-0.20	EBS_BLKI	-0.04
EBSATF	-0.21	CAK_CM	-0.05
WAK_CO	-0.21	SAK_CO	-0.05
CAK_CH	-0.22	GOAHAL	-0.05
WAK_SO	-0.22	EBSAKPLA	-0.10
GOAHAL	-0.22	GOAATF	-0.11
SAK_PI	-0.23	GOAPOP	-0.16
SAK_CM	-0.23	SAK_CH	-0.16
CAK_CO	-0.24	SAK_CM	-0.16
SAK_CO	-0.24	AIATKA	-0.18
CAK_PI	-0.24	EBSATF	-0.20
CAK_SO	-0.24	BSJELLY	-0.42

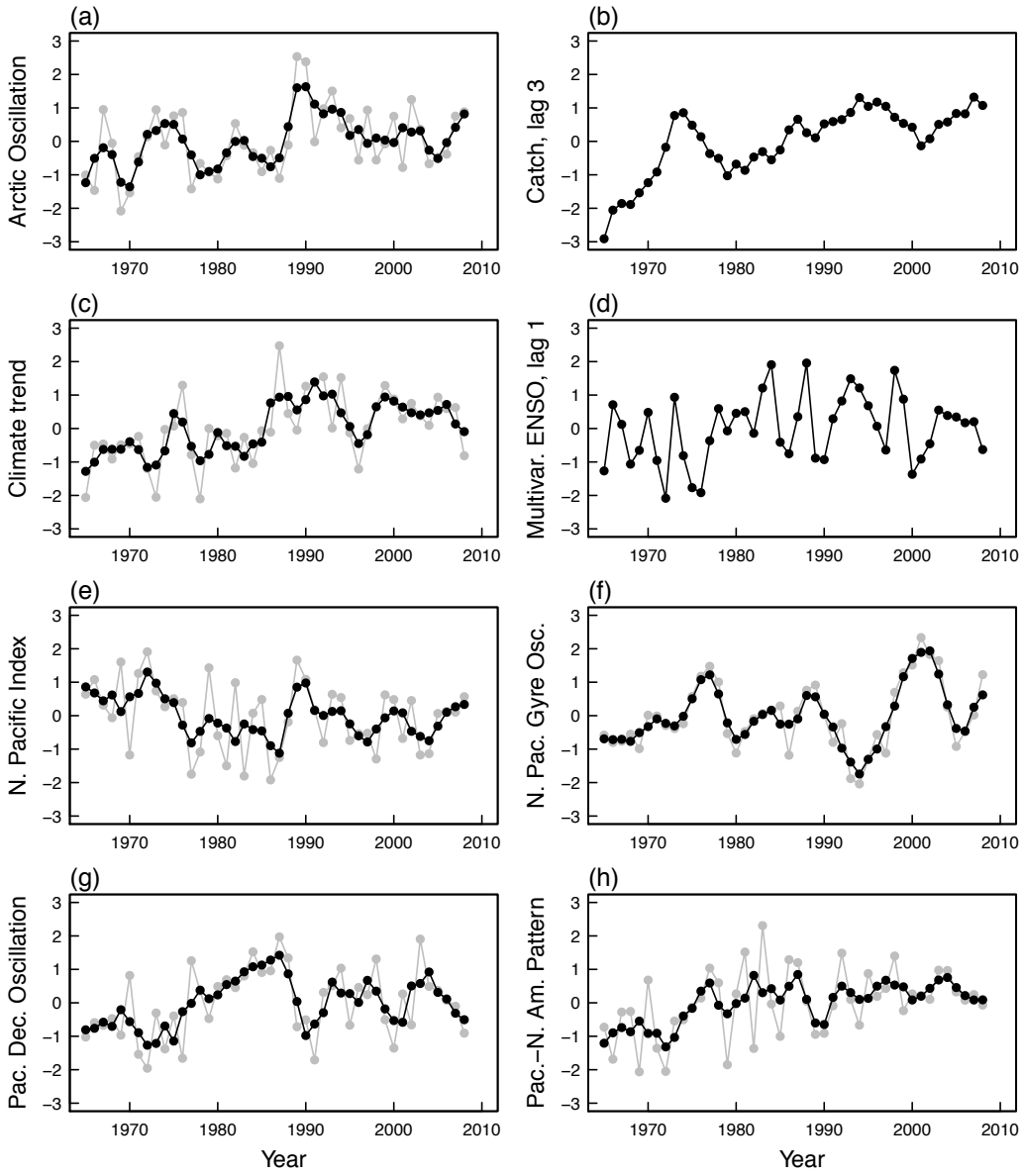

Fig. 1.S1 Time series of external forcing variables used in analysis of community variability, scaled as 0 mean, unit variance. Time series that were smoothed for analysis show both smoothed data (black) and raw data (gray).

Chapter 2 Assessing the ecological importance of climate regime shifts: an approach from the North Pacific Ocean

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Abstract

We used an indicator approach to address outstanding questions concerning the ecological importance of low-frequency climate variability in the northeast Pacific Ocean. Our data consist of a previously-published set of 33 climate and 64 biology time series, updated by us for the years 1965-2011 (for climate data) and 1965-2008 (for biology data). A model-selection approach showed that the first axis of variability in large-scale climate indices ($PC1_{ci}$), the first and second axes for local climate parameters ($PC1_{cp}$ & $PC2_{cp}$) and the second axis for biological variability ($PC2_{biol}$) all showed temporal variability best described by abrupt shifts. In contrast, $PC1_{biol}$ showed continuous, rather than abrupt, temporal variability, suggesting that the leading axis of biological variability was not dominated by abrupt transitions following climate regime shifts. The leading mode of variability in detrended North Pacific sea surface temperature, the Pacific Decadal Oscillation, showed reduced amplitude from the late 1980s until the mid-2000s, and we found that this change in PDO behavior was associated with a decline in the strength of the leading pattern of basin-scale biological variability ($PC1_{biol}$). A reversion to a PDO-negative state in the winter of 2007/08 was associated with the largest observed annual change in the $PC1_{bio}$-$PC2_{bio}$ phase space, suggesting renewed ecological importance of the PDO. However, a subset of biology time series (n = 23) for which more recent data were available did not show persistent change in $PC1_{bio}$ or $PC2_{bio}$ during 2008-2011, thus failing to support the hypothesis of widespread ecological response to the putative 2007/08 shift. To further assess the possible ecological importance of low-frequency climate variability in recent years, we compared changes in the PDO-North Pacific Gyre Oscillation (NPGO) phase space for 2007/08 with ecologically important (1976/77) and less important (1988/89) climate regime shifts of the past. We found that all three shifts involved PDO-NPGO variability of similar magnitude (i.e., similar pulse disturbances), but that the 1976/77 shift was followed by a period of stability in a new climate state (i.e., strong press disturbance), while the 1988/89 shift was not followed by a period of stability (weak press disturbance). Data through 2013 suggest that the press disturbance following 2007/08 is similar to that following 1976/77, implying that the putative 2007/08 shift may eventually prove to be ecologically

important. Our "pulse-press" approach provides a formal framework for distinguishing transient and persistent climate perturbations at the ends of time series.

Keywords: climate; ecosystem disturbance; fisheries; North Pacific Gyre Oscillation; Pacific Decadal Oscillation; regime shift

Introduction

Red noise in low-frequency climate variability in the North Pacific Ocean may produce decadal-scale periods of stability separated by sudden transitions (Rudnick and Davis 2003, Hsieh et al. 2005, Di Lorenzo and Ohman 2013). In the 1990s, it became widely accepted that these sudden climate transitions resulted in community-level, basin-scale biological reorganization (Francis and Hare 1994, Mantua et al. 1997, Benson and Trites 2002), and ecologists began commonly referring to these events as "regime shifts". The most familiar pattern of low frequency climate variability in the North Pacific is the Pacific Decadal Oscillation (PDO), the first empirical orthogonal function (EOF) of residual variability in North Pacific sea surface temperature (SST) fields, after the global warming signal is removed (Mantua and Hare 2002). The PDO is also characterized by variability in the intensity of the Aleutian Low (Minobe 1999, Di Lorenzo and Ohman 2013), and is mechanistically associated with El Niño-Southern Oscillation (ENSO, Newman et al. 2003).

While the climate regime shift concept was useful for understanding sudden historical biological reorganization events in the North Pacific in the 1940s and 1970s (Mantua et al. 1997, Hare et al. 1999), several problems limit the general utility of the concept in marine ecology. Most notably, a universally agreed-upon definition of regime shifts has never been established. Ecologists have tended to use *ad hoc*, system-specific definitions (Lees et al. 2006), and have applied models of abrupt transition without considering alternate models of temporal variability (Spencer et al. 2012). This failure to test hypotheses for more gradual change is an important gap in marine ecology, as regional-scale changes to climate are increasingly being attributed to anthropogenic forcing (Hegerl et al. 2007), such that the ecological importance of internal climate variability should progressively become overshadowed by that of anthropogenic climate change (Overland and Wang 2007).

A further hurdle in the application of the regime shift concept lies in the difficulty of using historical patterns of natural climate variability to understand contemporary climate-biology covariation. After quasi-stable states in the 20th century PDO pattern had been recognized, there was interest in the predictive capability offered by recognizing the next regime shift as it occurred, with particular attention paid to a 1998/99 change in sign of the PDO Index (e.g., Peterson and

Schwing 2003). However, the 1998/99 PDO shift proved to be a transient occurrence associated with ENSO, and not the beginning of a decadal-scale regime (Bjorkstedt et al. 2011). The 1998/99 experience highlights the difficulty in distinguishing transient disruptions from low-frequency variability at the ends of time series. This difficulty is exacerbated by non-stationary behavior in leading modes of natural climate variability; proxy records indicate that the PDO did not explain a leading proportion of North Pacific climate during the 19th century (Gedalof et al. 2002), and from 1989 until (at least) 2008, the PDO has been dominated by noise (i.e., shown reduced amplitude, autocorrelation and variability), while the second mode of detrended SST and sea surface height, the North Pacific Gyre Oscillation (NPGO), captured more climate variability (Bond et al. 2003, Di Lorenzo et al. 2008, Yeh et al. 2011). While it has long been recognized that 1988/89 was not a simple reversal of the 1976/77 event, both instances have been identified as regime shifts (Hare and Mantua 2000), emphasizing the difficulty in deriving a uniform definition for the term. The ecological implications of the decline in "regime" behavior of the PDO since 1988/89 have not, to our knowledge, been formally addressed. And finally, the difficulties in "real time" understanding of incipient low-frequency climate variability are again highlighted by a recent run of negative PDO values, beginning in 2007/08, and uncertainty over the persistence of associated climate anomalies (Cai and van Rensch 2012, Overland et al. 2012, Zwolinski and Demer 2012).

Because the mechanisms underlying climate-biology links are still imperfectly understood, statistical patterns of climate-biology covariation over large spatial scales have often been used to elucidate biological responses to climate regime shifts in the North Pacific (Mantua et al. 1997, Hare and Mantua 2000, Boeing and Duffy-Anderson 2008). In this study, we use leading axes of ecological variability in the northeast Pacific Ocean during 1965-2011, as defined by a well-known set of ecosystem indicators (33 climate and 64 biology time series; Hare and Mantua 2000), to address outstanding questions concerning the role of climate regime shifts in the North Pacific. Our specific goals were to: 1) provide an updated perspective on climatic and biological variability at the scale of the northeast Pacific; 2) determine whether leading axes of variability were better described by abrupt or gradual models of temporal variability; 3) test the hypothesis that changes in the statistical behavior of the PDO index change the strength of the leading axis of variability in our biological time series; and 4) compare climatic and biological changes across 2007/08 with

earlier events in order to evaluate the evidence for an ecologically-important shift to a new climate regime in the North Pacific.

Finally, because a standardized definition for "regime shifts" in marine ecology has proven elusive (Lees et al. 2006), we define our conceptual approach and use of the term here. To some degree, the absence of a consensus definition for regime shifts arises from differences in application of the concept in climate science and oceanography on one hand, and ecology on the other. A consensus has built over the last decade that occasional abrupt shifts in the mean state of fundamental climate parameters is most parsimoniously explained by autocorrelated stochastic variability (i.e., red noise) that arises from integrating underlying white noise processes (Rudnick and Davis 2003, Hsieh et al. 2005, Di Lorenzo and Ohman 2013). An important implication of this view is that the timing of these shifts is not predictable, so that attempts to define periodicity in leading modes of low-frequency climate variability (e.g., Minobe 1999, Zwolinski and Demer 2012) are likely to be unsuccessful. On the other hand, regime shifts in ecology refer to abrupt shifts between alternative stable states that are separated by hysteresis (state-dependent forcing-response relationships); ecological regime shifts are seen as the result of both incremental perturbations that gradually reduce system resilience and an abrupt stochastic perturbation that initiates the shift (Scheffer et al. 2001). Ecological regime shifts have been ascribed to a variety of perturbations, including overfishing, eutrophication, habitat alteration and climate variability (deYoung et al. 2008, Möllmann and Diekmann 2012). However, demonstrating the presence of alternate stable state dynamics from observational data is challenging (Schröder et al. 2005, Hsieh et al. 2008a), and abrupt ecological changes that have been heuristically identified as regime shifts between alternative stable states (e.g., in the Scotian Shelf and a variety of coral reef ecosystems; Knowlton 1992, Scheffer et al. 2001, Choi et al. 2004, deYoung et al. 2008) can more parsimoniously be explained by other phenomena (e.g., phase shifts and ecological transients; Petraitis and Dudgeon 2004, Dudgeon et al. 2010, Frank et al. 2011). Since formal tests for alternative stable states are beyond the scope of this paper, we refrain from using the term "regime shift" to describe biological variability. However, while red noise-associated shifts in low-frequency climate variability are inherently unpredictable, such shifts in climate are expected to remain important drivers of marine ecosystem variability (Overland and Wang 2007),

and we refer to these abrupt changes as "climate regime shifts" for the sake of convenience.

Materials and methods

Data

We updated the climate time series from the Hare and Mantua (2000) study for the years 1965-2011, and, because recent biology data were often unavailable, we updated biology time series for 1965-2008. The original Hare and Mantua (2000) data covered the period 1965-1997, so our updates represent a 33-42% increase in time series length. Sources, descriptions and scientific names for all time series are presented in Table 2.S1, and further information is available in Hare and Mantua (2000). Six time series from the original paper (Eastern Bering Sea zooplankton biomass, Eastern Bering Sea Pacific Ocean perch recruitment, Gulf of Alaska shortspine thornyhead recruitment, central Pacific zooplankton biomass, West Coast yellowtail rockfish recruitment, California coho salmon catch) are, to the best of our knowledge, no longer maintained, and were not used in our analysis. In two other instances, we were able to replace discontinued time series with other time series that convey similar ecological information from the same general location (West Coast anchovy recruitment replaced with West Coast sardine catch; east Pacific zooplankton biomass replaced with combined Ocean Station Papa/Vancouver I. zooplankton phenology; details in Table 2.S1). We also excluded Washington pink salmon catches from our analysis, as this fishery only operates in alternate years. Finally, we added two biology time series (British Columbia herring recruitment and shrimp catch) that were not included in the original study.

Climate time series from Hare and Mantua (2000) include both large-scale climate indices (e.g., PDO Index) and climate parameters that were measured at single locations (e.g., SST). Because these two types of time series measure climate variability at different scales (i.e., basin- or hemisphere-scale indices vs. local-scale parameters), we separated the two groups for analysis. Local-scale climate parameters were fairly evenly divided among time series of SST (four), air temperature (six), river volume (five) and upwelling strength (six), and also include a measure of seasonal Bering Sea ice cover and winter surface advection vectors from Ocean Station Papa. Climate indices were dominated by time series measuring

variability in the PDO, Arctic Oscillation (also known as the Northern Annular Mode), Southern Oscillation and North Pacific sea level pressure variability (SLP; measured by the North Pacific Atmospheric Index of Hare and Mantua [2000], the average of the standardized North Pacific Index, Pacific North American Pattern and Aleutian Low Pressure Index). The NPGO, which was not recognized at the time of the original study, captures variability in the strength of gyre circulation, upwelling, and horizontal advection in the North Pacific (Di Lorenzo et al. 2008), and we added both winter and summer values of the NPGO Index to the data set. The updated data set therefore included 97 time series: ten large-scale climate index time series, 23 local climate parameter time series and 64 biology time series (Fig. 2.1).

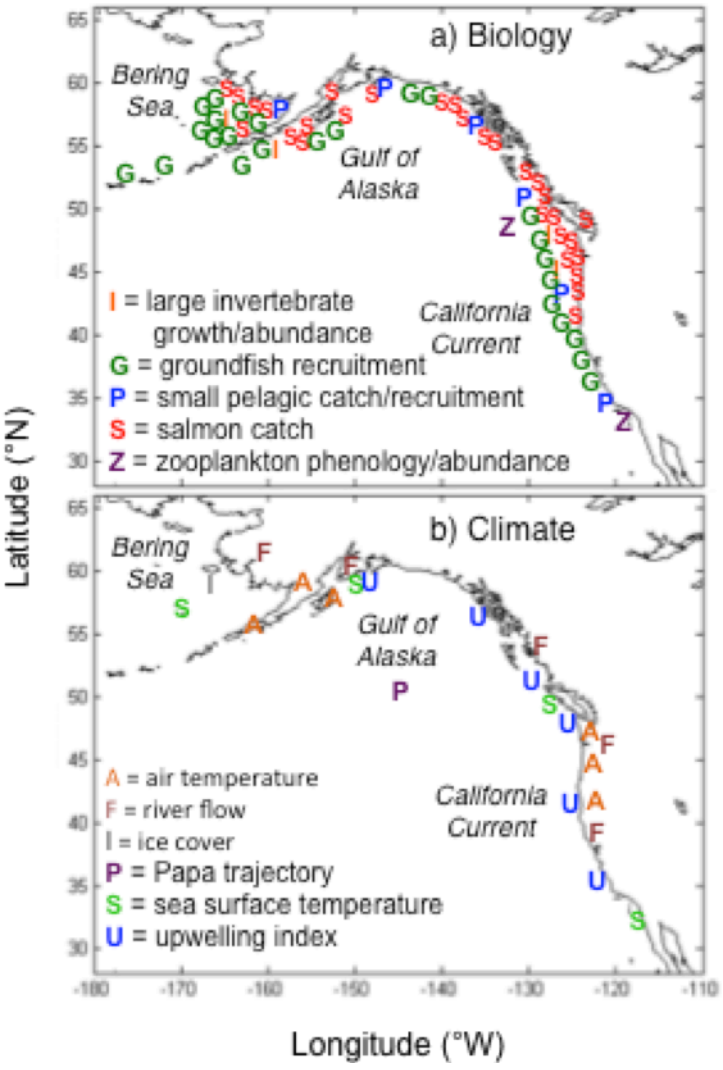

Fig. 2.1 Approximate location of time series used in analysis. Locations for large-scale climate indices not indicated.

Biology time series were dominated by commercially important fish populations. Twenty-eight were time series of commercial salmon catches, log-transformed and lagged to year of ocean entry, and another (the Northern Diversion Rate) was a measure of migration behavior for British Columbia sockeye salmon. Twenty-three were time series of groundfish recruitment estimates, log-transformed and lagged to cohort year, and another six were recruitment estimates or catches for small pelagic fishes, log-transformed and lagged to cohort year. Four other time series were

measures of macro-invertebrate abundance or growth, and two time series measured zooplankton biomass or phenology.

Analysis

Leading axes of ecological variability

We summarized leading axes of ecological variability with principal components analysis (PCA) run separately on large-scale climate indices (PC_{ci}), local climate parameters (PC_{cp}), and biology time series (PC_{biol}). Missing values (4.3% of total) were estimated using multiple imputation with Bayesian linear regression techniques implemented in the MICE package (Van Buuren and Oudshoorn 1999) in the computer language R (R Development Core Team 2010). Multiple imputation consisted of five iterations, each consisting of 100 imputations. Mean PC scores and associated standard deviation (SD) values for every year with missing time series values were estimated from the distribution of the 100 imputed values from the final iteration. We then identified the number of interpretable axes from our PCA results using the broken-stick approach of Jackson (1993), but limited our analysis to no more than the first two PCs in order to concentrate on the most important modes of variability. We interpreted the variability captured by leading PC scores in terms of the strongest time series loadings (absolute loading values ≥ 0.2 for climate PCA, and ≥ 0.15 for biology PCA).

Abrupt vs. gradual models of variability

We used a model selection approach to determine whether observed ecological variability was better described by gradual change or abrupt shifts between steady states. To construct abrupt shift models, we began by using STARS (sequential t-test analysis of regime shifts; Rodionov 2006) to identify shift points in time series. For STARS tests we set $\alpha = 0.05$; the length of the proposed regimes, $L = 15$ years to match the approximate frequency of previously documented climate regime shifts in the data set (Hare and Mantua 2000); and the Huber weight parameter, $H = 6$ SD, which had the effect of treating extreme time series values as representative, rather than as outliers. To account for temporal autocorrelation, we reduced effective degrees of freedom for these tests with the IP4N method, using the median value of AR1 estimates calculated from all possible 5-year windows in the time series in

question (Rodionov 2006). These results are presented with the notation *P′*. We did not prewhiten time series before STARS analysis out of concern over a potentially unacceptable increase in Type-II error rates (Pyper and Peterman 1998). STARS explicitly models time series variability as shifts between stable mean states (Rodionov 2006), so we used ANOVA with STARS-defined regime identity as a class variable for modeling time series variability.

Gradual change in time series was modeled with generalized additive models (GAMs), using year as the explanatory variable. GAMs utilized a Gaussian distribution and identity link and smooth functions were estimated with penalized regression splines as implemented in R package mgcv (Wood 2008). We limited GAM smoothing (effective degrees of freedom [EDF] ≤ 5) in order to avoid over-fitting and to allow for approximately decadal-scale trends in the time series. Model selection (ANOVA vs. GAM) was conducted with Akaike's Information Criterion controlled for small sample size (AICc). Selection of the ANOVA model was taken as support for abrupt shifts between STARS-defined states, while selection of the GAM was taken as support for gradual variability in a time series.

Amplitude as a measure of ecosystem importance of the PDO

While change in the "regime" behavior of the PDO might be indicated by changes in a suite of statistical parameters (e.g., amplitude, SD, AR1 coefficients), we used amplitude (average absolute value) as our metric for the sake of consistency with earlier studies (Bond et al. 2003, Yeh et al. 2011). Specifically, we tested the hypothesis that a decline in amplitude of the winter (NDJFM) PDO was associated with a decline in the strength of the community-level biological response to the PDO. Our response variable in this analysis was the average correlation strength between the individual biological time series and $PC1_{biol}$, calculated on a 15-year sliding window to match the length of *L* in STARS analysis. This PC score tracks the large-scale biological responses that have previously been associated with PDO forcing (*section 3.1*), and we reasoned that the 15-year moving average of correlation strength between the PC score and its component time series provides a measure of the amount of variability associated with the leading PC axis. PDO amplitude was also calculated as a 15-year moving average. The correlation between PDO amplitude and the biological response variable was analyzed with the Modified Chelton method to account for autocorrelation (Pyper and Peterman 1998), and we use the notation *n′*

and P' to report the adjusted sample size and probability, respectively, for this analysis.

Outlook for an ecosystem shift in the 2000s

Biology

We began evaluating the possible biological response to the putative 2007/08 climate regime shift size by comparing the 2007/08 change in the $PC1_{biol}$-$PC2_{biol}$ phase space with changes during the rest of the time series. Phase space change between year *t* and year *t-1* was calculated as the length of the hypotenuse created by vectors on the $PC1_{biol}$ and $PC2_{biol}$ axes:

$$\text{total change} = \sqrt{\left(PC1_t - PC1_{t-1}\right)^2 + \left(PC2_t - PC2_{t-1}\right)^2}.$$

We tested the hypothesis that the 2007/08 change was the largest in the entire time series using an *ad hoc* randomization approach that accounted for the uncertainty in our estimates of PC scores in years with missing time series values. Note that this approach assumes that uncertainty for PC scores in years with no missing values is negligible. The analysis followed three steps:

1) We created 1000 randomized, paired $PC1_{biol}$, $PC2_{biol}$ time series for the years 1965-2008. For years when no time series values were missing, PC scores were fixed at the observed level. For years with missing values, PC scores were randomly drawn from a normal distribution defined by the mean and SD for each PC score for the year in question, as estimated by multiple imputation (*section 2.2.1*).
2) We calculated the change in the $PC1_{biol}$-$PC2_{biol}$ phase space for each of the 43 year-to-year changes in all 1000 randomizations.
3) We used standard normal probabilities (*z*-scores) to test the null hypothesis that the 2007/08 change came from the same distribution as the other 42 year-to-year changes, with separate *z*-scores calculated for all 1000 randomizations. The average of all *z*-scores was used to estimate the probability that the 2007/08 change came from the same distribution as the other year-to-year changes, given the uncertainty around PC scores for years with missing values.

Climate

A central question for the putative 2007/08 shift, or any other possible climate regime shift, is whether post-shift climate anomalies will last long enough to cause lasting ecological change. We calculated the SD of winter (NDJFM) PDO Index values on a 10-year moving window (i.e., the longest window that could be calculated to span the 2007/08 event with available data), and examined the resulting time series for characteristics that might distinguish ecologically important shifts (e.g., 1976/77) from less ecologically important shifts (e.g., 1988/89). The resulting time series of PDO variability (Fig. 2.2) suggests that ecologically important shifts are characterized by a sharp peak in variability of the climate variable of interest, indicating high variability centered on the shift event (i.e., a strong pulse disturbance), and lower variability after the event, consistent with maintenance of post-shift conditions (i.e., a persistent press disturbance). Based on these observations, we compared the pulse and press characteristics of 2007/08 with 1976/77 and 1988/89 in order to evaluate the possible ecological importance of this most recent event. We used winter (NDJFM) values of both the PDO and NPGO indices in this analysis, as ecologically important change in the PDO tends to coincide with change in the NPGO (Di Lorenzo et al. 2008). We compared the size of the pulse disturbance (i.e., variability across the shift) using the average SD for the PDO and NPGO during 10-year windows centered on the events of interest. Only 5 years of data (2008-12) were

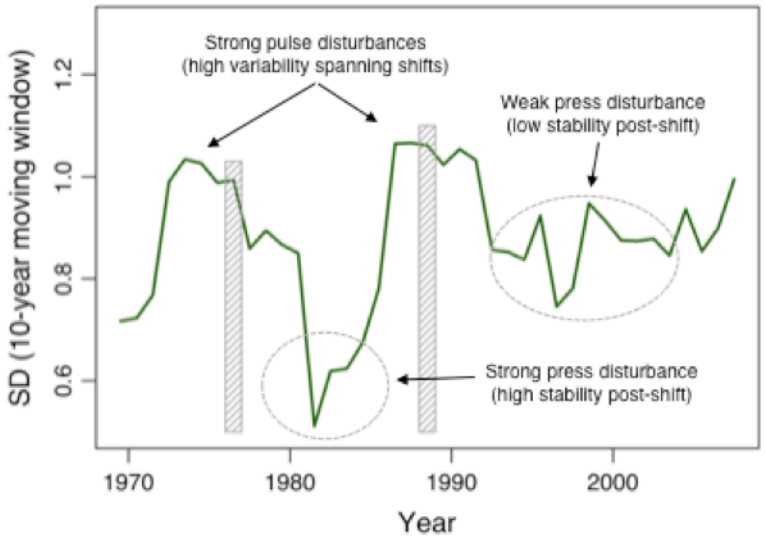

Fig. 2.2 Rationale for the "pulse-press" approach for assessing the potential ecological importance of abrupt climate shifts – an example with the winter (NDJFM) PDO Index. Plotted data (green line) is PDO variability (SD) on a 10-year moving window, centered on the year plotted. Cross-hatching indicates 1976/77 and 1988/89 climate shifts. Note that the ecologically important (1976/77) and less-important (1988/89) shifts are characterized by similar pulse disturbances (high variability across each shift), but the 1976/77 event is followed by a period of stability in the "new" climate state (strong press disturbance), while the 1988/89 event is characterized by less stable post-shift conditions (weak press disturbance).

available to characterize the press disturbance (i.e., variability following the shift) for the putative 2007/08 event, so we used 5-year SD values to compare mean PDO-NPGO variability among different post-shift climate regimes (1965-1976, 1977-88, 1989-2007, 2008-12). Values for the winter 2013 PDO, but not the winter 2013 NPGO, became available while this paper was in review. In the interest of extending our analysis of post-2007/08 stability through an additional year, we estimated the 2013 NPGO using multiple imputation with JAS values of the NPGO and NDJFM values of PC2 of detrended North Pacific SST (from the ERSSTv.3b data set) as predictor variables. The resulting estimate of the winter 2013 NPGO (1.05, 95% CI = -0.27 - 2.36), allowed us to estimate SD for two 5-year windows following the putative 2007/08 shift. Different 5-year SD values within individual regimes violated assumptions of independence, so we used a randomized ANOVA (Manly 2006) to test the null hypothesis that SD values did not differ among the regimes. We resampled the PDO and NPGO time series, with replacement, 1000 times, calculated SD values for 5-year windows for each of the permutations, and calculated the proportion of permutations with *F*-statistics more extreme than that observed in the actual data. Pairwise differences between regimes were tested for significance by comparing standard normal probabilities (*z*-scores) for pairwise differences from the observed data with pairwise differences from the 1000 random permutations. As randomized permutations for the NPGO time series included the distribution of 2013 values produced by multiple imputation, this randomization procedure accounts for uncertainty associated with estimating that value.

Results

Leading axes of ecological variability

The PCA of large-scale climate index time series returned one interpretable axis ($PC1_{ci}$), which explained 34% of total variance, with negative loadings for the Southern Oscillation Index and summer and winter values of the NPGO Index, and positive loadings for the East Pacific/North Pacific teleconnection index, the North Pacific Atmospheric Index, summer and winter values of the PDO Index, and winter ENSO values (Fig. 2.3a).

The PCA of local climate parameter time series produced four interpretable axes. The first two PCs explained 27% and 14% of total variance, respectively, 1.4

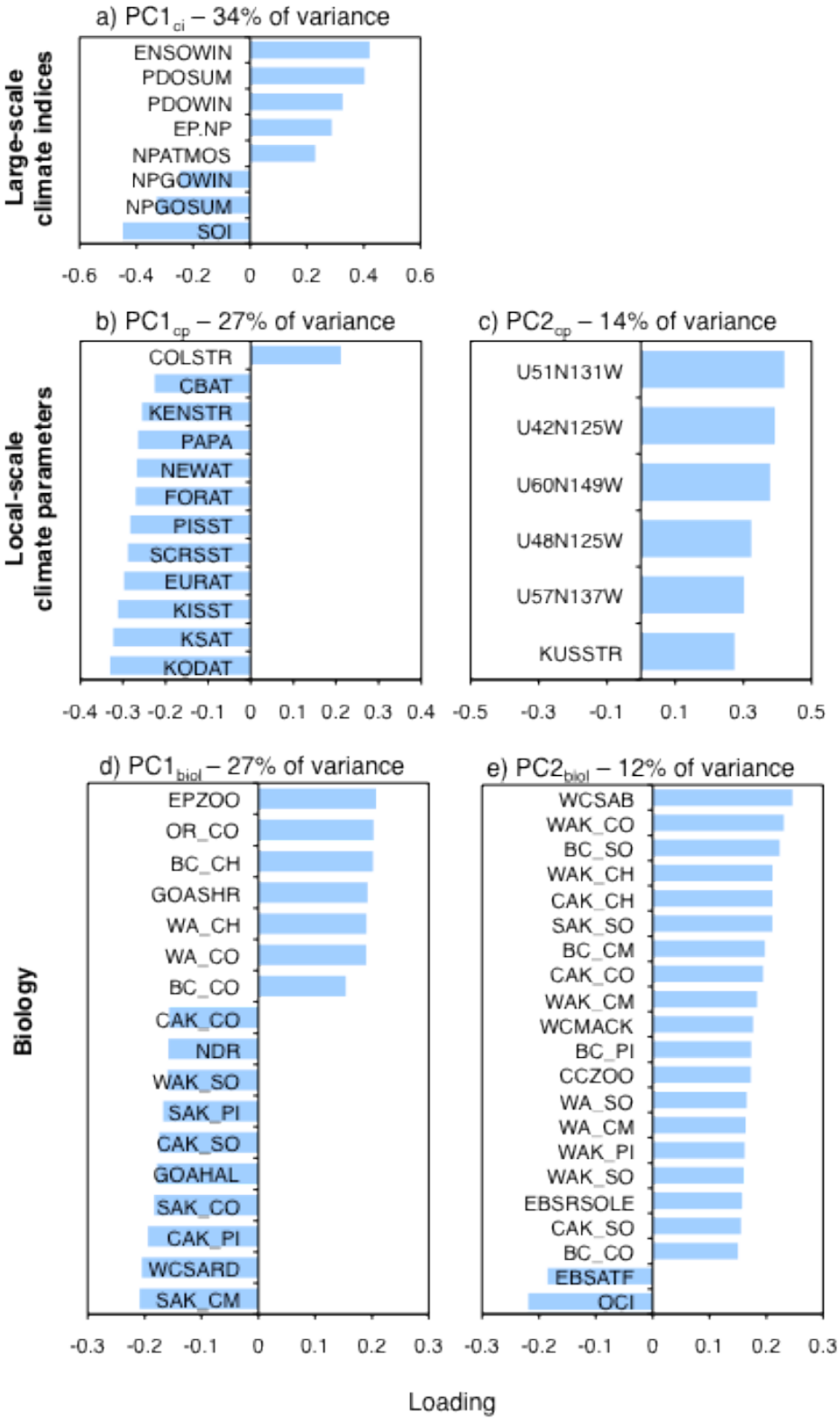

Fig. 2.3 Leading modes of ecological variability in the northeast Pacific Ocean: strongest PCA loadings for (a) large-scale climate indices; (b, c) local climate parameters; (d, e) biology time series.

times the amount expected for the first two PCs under the broken-stick distribution. The first PC ($PC1_{cp}$) had negative loadings for nine air and sea surface temperature time series from southern California to the Bering Sea, as well as for the Ocean Station Papa trajectory index and Kenai River stream flow, and was positively correlated with Columbia River stream flow (Fig. 2.3b). $PC2_{cp}$ was dominated by upwelling variability: five upwelling indices (all but the southernmost in the study) had positive loadings, as did Kuskokwim River stream flow (Fig. 2.3c).

Table 2.1 Summary of model selection results for Principle Component (PC) time series.

Data set	PC score	STARS-defined shifts year(*P'*)	STARS-estimated AR1	GAM EDF	GAM Δ-AICc	ANOVA Δ-AICc
Climate indices	$PC1_{ci}$	1977(0.0007) 2008(0.02)	0.13	2.65	6.8	0
Climate parameters	$PC1_{cp}$	1977(<0.0001) 2007(0.006)	0.00	2.19	13.6	0
	$PC2_{cp}$	1983(0.0002) 1998(0.03)	0.00	3.20	3.9	0
Biology	$PC1_{biol}$	1980(0.051)	0.99	4.64	0	42.5
	$PC2_{biol}$	1977(0.0009) 1996(0.0008)	0.79	4.57	14.1	0

The biology time series PCA produced five interpretable axes, and the first two axes explained 27% and 12% of total variance, respectively, 2.9 times that expected under the null distribution. $PC1_{biol}$ captured the "inverse production regimes" between Alaskan and West Coast salmon populations; seven Alaskan salmon time series showed negative loadings, while five salmon time series from the West Coast showed positive loadings (Fig. 2.3d). $PC1_{biol}$ also expressed the tradeoff between East Pacific zooplankton phenology and Gulf of Alaska shrimp catches (positive loadings) versus values of the Northern Diversion Rate, Gulf of Alaska halibut recruitment and West Coast sardine catch (negative loadings). $PC2_{biol}$ was dominated by positive loadings on salmon time series, both from Alaska (nine time series) and the West Coast (six time series). $PC2_{biol}$ also showed positive loadings on California Current zooplankton abundance and recruitment for West Coast sablefish, West Coast mackerel and Bering Sea rock sole; and negative loadings on Bering Sea arrowtooth flounder recruitment and the Washington Oyster Condition Index (Fig.

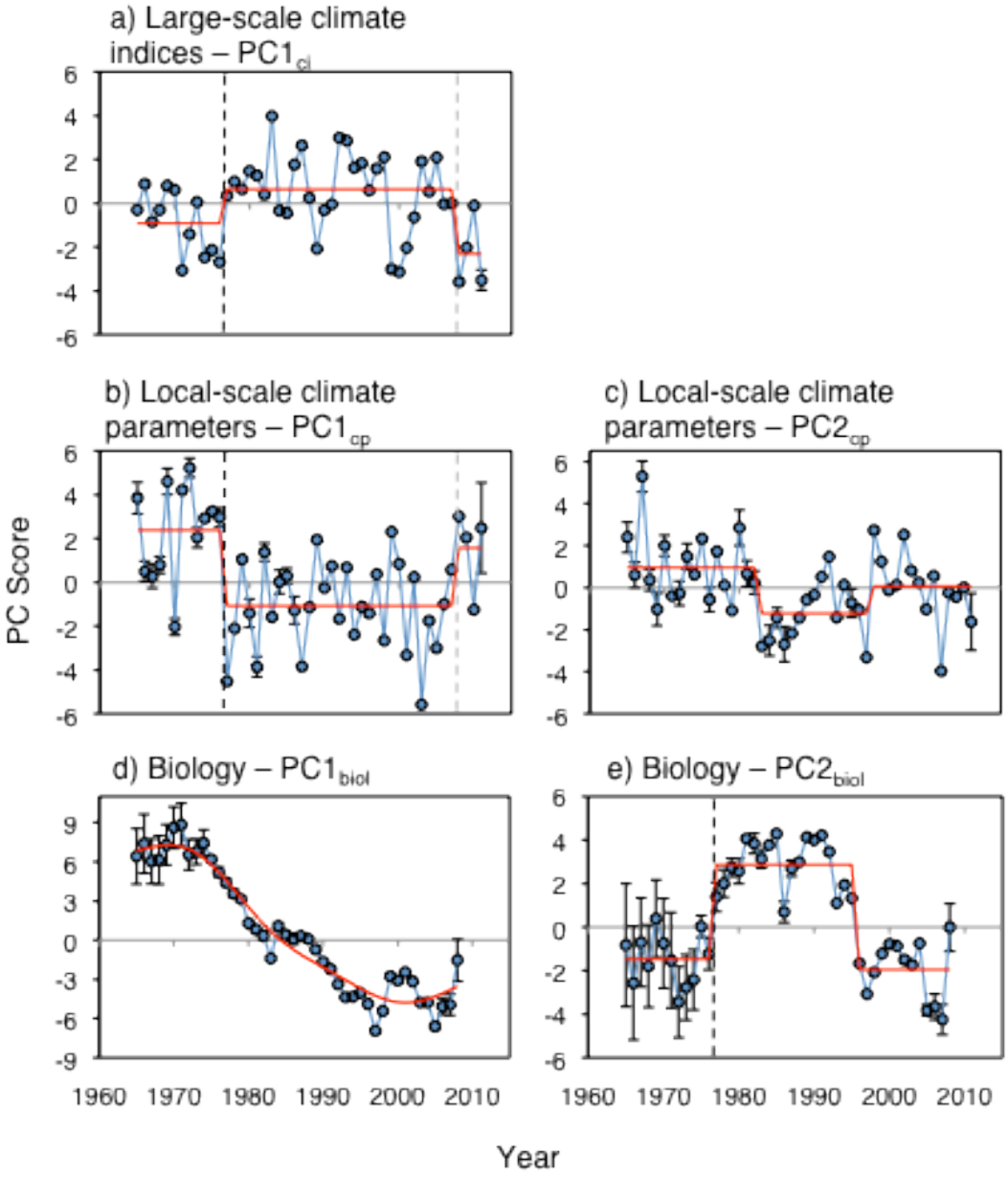

Fig. 2.4 Leading modes of ecological variability in the northeast Pacific Ocean: PCA time series. Blue circles indicate observations, red lines indicate best models for temporal variability: threshold (STARS/ANOVA; a-c, e), or gradual (GAM, d), as determined by AIC. Error bars = 95% CI, and reflect uncertainty associated with estimating missing values. Dashed black vertical line indicates simultaneous changes in 1976/77, dashed grey vertical line indicates 2007/08.

2.3e). Complete PCA loadings are presented in Tables 2.SP.2-2.SP.4.

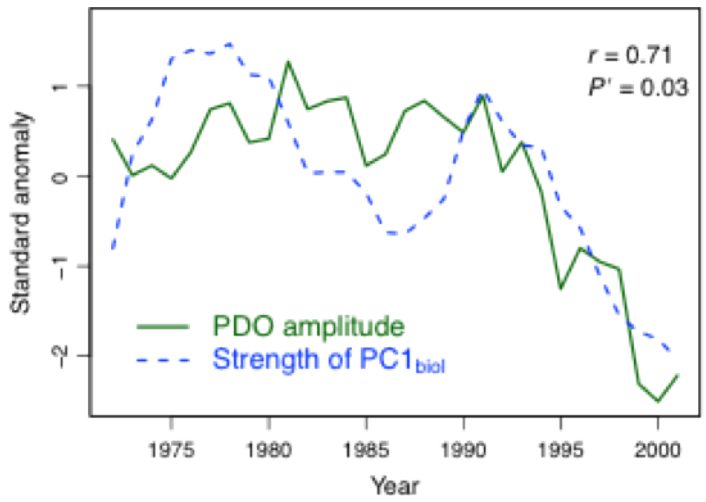

Fig. 2.5 Patterns and consequences of changing behavior in the PDO: time series of PDO amplitude (mean absolute value) and strength of $PC1_{biol}$ (average Pearson's $|r|$ between individual time series and PC score). Both time series calculated on a 15-year sliding window to match the length of L in STARS analysis, and standardized as mean 0, unit variance.

Abrupt vs. gradual models of variability

STARS identified one or two shift points in each PC time series (Table 2.1), and ANOVA models that expressed temporal variability as STARS-defined shifts among steady states were the best models (lowest AICc scores) for four PC time series ($PC1_{ci}$, $PC1_{cp}$ & $PC2_{cp}$, $PC2_{biol}$, Fig. 2.4). A model of gradual temporal variability (GAM with limited smoothness) was the best model only for the first axis of biological variability ($PC1_{biol}$, Fig. 2.4d). Model selection produced generally large values of Δ-AICc, indicating strong support for the best model in each case (Table 2.1).

PDO behavior as a measure of ecosystem forcing

We found that variability in PDO amplitude predicted the strength of $PC1_{biol}$. PDO amplitude declined precipitously beginning in the mid-1990s, corresponding to the first 15-year windows consisting entirely of data following the 1988/89 shift (Fig. 2.5). This change in PDO behavior in turn had a linear relationship with the strength of $PC1_{biol}$ ($r = 0.71$, $P' = 0.03$).

Assessing the putative 2007/08 climate shift

Biology

$PC1_{biol}$ and $PC2_{biol}$ both showed noticeable departures from previous mean values in 2008, the last year that these PC scores could be estimated for the full set of

biology time series, though single-year departures were not sufficient to establish new STARS-defined states (Fig. 2.4d, e). The magnitude of the estimated 2007/08 change in the $PC1_{biol}$-$PC2_{biol}$ phase space (5.51 units) was 311% that of the 1966-2007 mean (Fig. 2.6). In each of the 1000 randomizations, the 2007/08 change was significantly different from the other 42 year-to-year changes (smallest z-score in the 1000 randomizations = 2.95, corresponding to $P = 0.002$). The average z-score across all randomizations was 5.53, corresponding to $P < 0.00001$, and providing very strong support for the alternate hypothesis that the 2007/08 $PC1_{biol}$-$PC2_{biol}$ change was larger than any other year-to-year change in the time series, even when uncertainty due to missing values was taken into account.

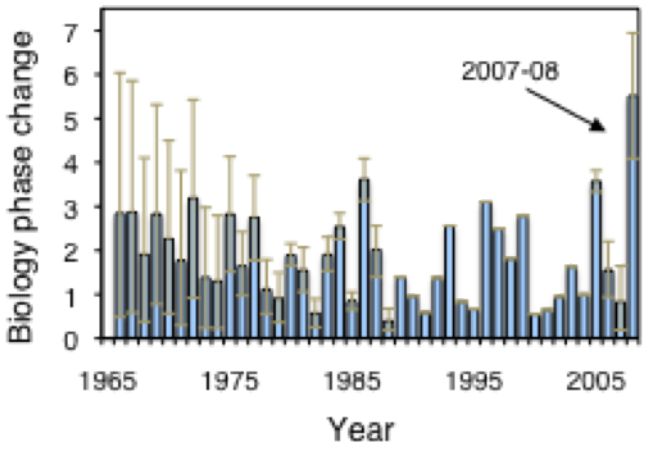

Fig. 2.6 Year-to-year changes in leading axes of northeast Pacific biological variability: Each year plots total change in $PC1_{biol}$-$PC2_{biol}$ phase space from previous year. Error bars = 95% CI, indicating uncertainty from estimating missing time series variables. The 2007/08 change was 311% of the mean across all other years in the time series ($z = 5.53$, $P < 0.00001$).

Using a separate round of PCA and multiple imputation on a subset of biology time series ($n = 23$, Table 2.S1) that could be updated at least through 2010, we were able to estimate biology PC scores through 2011 to make inferences about the persistence of the dramatic $PC1_{biol}$-$PC2_{biol}$ change in the full data set. The two leading PCs were well correlated for the full and restricted data sets for the years of overlap (i.e., 1965-2008; $PC1_{biol,}$ $r = 0.97$; $PC2_{biol,}$ $r = 0.92$, Fig. 2.7), indicating that the restricted data set tracked leading modes of variability from the full data set. STARS analysis of the extended biology time series failed to support the hypothesis of a shift in mean state for either $PC1_{biol}$ or $PC2_{biol}$ following 2007/08 ($P' > 0.2$, Fig. 2.7), suggesting that the 2007/08 change was not the beginning of a persistent, dramatic change in community state.

Climate

STARS showed a shift in mean values for axis 1 of large-scale climate indices ($PC1_{ci}$) during 2007/08 ($P' = 0.02$, Fig. 2.4a), and a shift in axis 1 of local climate parameters ($PC1_{cp}$, $P' = 0.006$, Fig. 2.4b) in 2006/07. Recent years in the PDO-NPGO phase space show an apparent transition to a PDO negative, NPGO-positive state since 2007/08 (Fig. 2.8a).

The size of pulse perturbations (average of 10-year SD for PDO and NPGO) was similar for the 1976/77 (0.96), 1988/89 (0.99) and 2007/08 (0.99) shifts. However, the persistence of the subsequent press perturbations (mean 5-year SD) was very different among the post-shift regimes (randomized ANOVA, $P = 0.03$). Specifically, the 1965-76 and 1977-88 regimes had a significantly lower mean PDO-NPGO variability than did the 1989-2007 period (1965-1976 vs. 1989-2007: $P = 0.01$; 1977-1988 vs. 1989-2007: $P = 0.01$, Fig. 2.8b). Additionally, the 2008-13 period, which included the estimated value for the 2013 NPGO, had lower variability than 1989-2007 ($P = 0.03$).

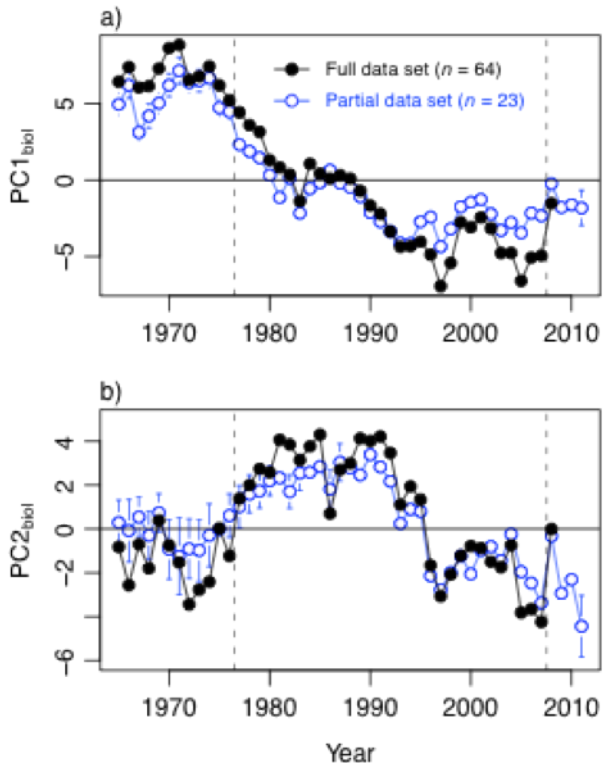

Fig. 2.7 Assessing the persistence of post-2007/08 change in (a) $PC1_{biol}$, and (b) $PC2_{biol}$, using a partial set of biology time series that could be updated at least through 2010. Error bars for PC scores calculated from partial data sets = 95% CI, and reflect uncertainty associated with estimating missing values. Time series for PC scores from full data set are plotted for comparison, with error bars omitted for clarity. Dashed vertical lines indicate 1976/77 climate regime shift and putative 2007/08 shift. STARS failed to detect a shift following 2007/08 for either PC time series calculated from the partial data set ($P' > 0.2$).

Discussion

Anthropogenic warming of North Pacific surface waters has become apparent over the past ~40 years, and is expected to intensify in coming decades (Hegerl et al. 2007). However, the PDO spatial pattern in North Pacific SST is reproduced by a number of general circulation models (GCMs), and predictions of continued importance of the PDO during the 21st century have been derived from ensemble projections using GCMs that were skillful in producing the 20th century PDO pattern

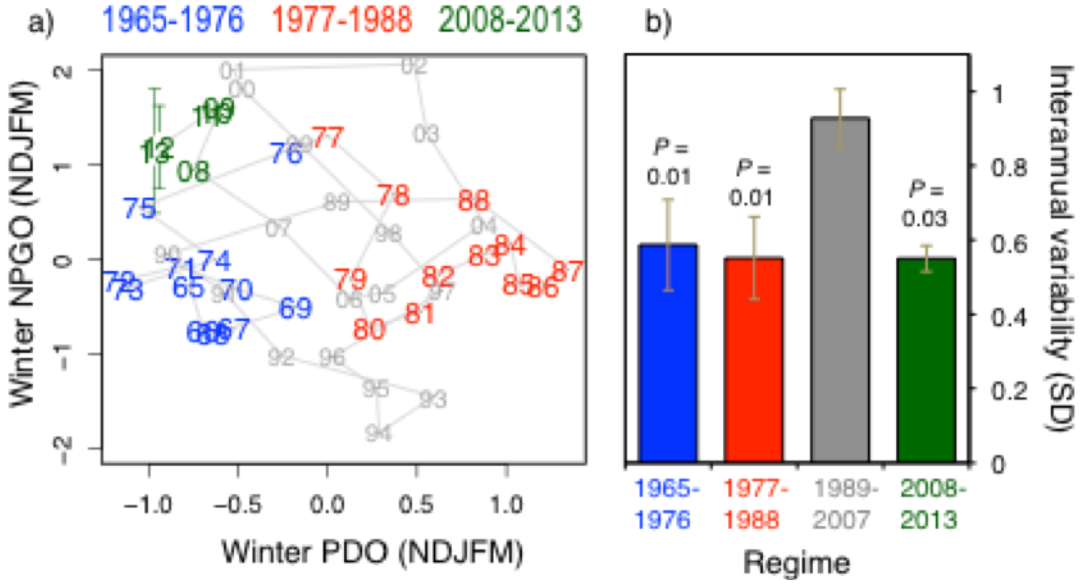

Fig. 2.8 Variability in the PDO and NPGO across 2007/08, relative to historical shifts. (a) NPGO-PDO phase space. Data are smoothed with a 3-year running mean to isolate the trend from noise, except for 2013, which is a 2-year running mean. Colors group earlier climate regimes (1966-1976 and 1977-1988) and recent years (2008-2013). Error bars = 95% CI, and reflect uncertainty associated with estimating 2013 NPGO value. (b) Press perturbations for four possible PDO-NPGO regimes: average SD calculated for every 5-year window in each regime, error bars = 95% CI. Note that lower SD values indicate a stronger press disturbance. Plotted *P*-values are pairwise comparisons with 1989-2007 variability, derived from randomized ANOVA.

(Overland and Wang 2007). An alternate view is given by observations of 21st century declines in PDO variance, and increases in NPGO variance, in GCM projections (Di Lorenzo et al. 2008), suggesting that the reductions in PDO variance and amplitude observed in recent decades (Fig. 2.5) are part of a long-term change. In this context, the recent run of consistently negative PDO values (Fig. 2.8a) is noteworthy, as it has been interpreted by some as an indication of a switch to a negative PDO state (Cai and van Rensch 2012), and a resumption of strong PDO effects on black-legged kittiwake (*Rissa tridactyla*) diet and reproductive success in

the Gulf of Alaska (Hatch 2013) and Pacific sardine recruitment in the California Current (Zwolinski and Demer 2012, Deyle et al. 2013), but see MacCall et al. (2012).

While it is unsurprising that the first PC of large-scale climate indices ($PC1_{ci}$) was better described by threshold, rather than gradual, modes of temporal variability (Overland et al. 2010, Di Lorenzo and Ohman 2013), our finding that $PC2_{biol}$, $PC1_{cp}$ and $PC2_{cp}$ were best described by threshold models confirms the importance of abrupt change events in North Pacific ecology since 1965 (Fig. 2.4). On the other hand, $PC1_{biol}$ was much better described by a gradual, rather than threshold model (Δ-AICc = 42.5, Fig. 2.4d). Although our analysis cannot distinguish between biological tracking of incremental change in forcing mechanisms and gradual transitions to equilibrium following perturbation (e.g., Frank et al. 2011), our observation of gradual change in this leading axis of biological variability both underscores the need to consider incremental forcing mechanisms such as habitat loss, fishing and anthropogenic climate change in attempts to understand basin-scale patterns of biological variability, and the dangers of applying abrupt shift models uncritically to all instances of dramatic change in time series (Spencer et al. 2012). In particular, the salmon populations that dominate $PC1_{biol}$ (Fig. 2.3d) have been negatively affected by incremental degradation of freshwater habitat over the southern part of their range during our study period (Nehlsen 1997). In Alaska, a linear climate trend of rising SST, decreasing SLP and rising freshwater input, independent of leading modes of internal climate variability, shows a strong statistical relationship with $PC1_{biol}$ variability (Litzow et al. 2014), suggesting another potential source of gradual change in $PC1_{biol}$. Thus, while PDO variability may continue to play an important role in driving biological variability in the northeast Pacific, especially with an apparent resumption in PDO forcing following 2007/08 (Fig. 2.8), a view of the PDO as the dominant factor in explaining biological variability in the region may not be tenable.

While the $PC1_{biol}$ time series was not dominated by abrupt shifts, we did find correspondence between the amplitude of the PDO and the strength of $PC1_{biol}$, as measured by the average strength of correlation with individual time series (Fig. 2.5). Studies of the ecological effects of climate regime shifts have typically concentrated on coherent shifts in climate and biology time series (e.g., Mantua et al. 1997, Hare and Mantua 2000, Benson and Trites 2002); to our knowledge, this approach of

evaluating the association between the strength of a climate signal and the strength of the biological response is unique. Change in the strength of $PC1_{biol}$ (Fig. 2.5) implies non-stationary patterns of ecological variability in the North Pacific that are coincident with a shift in the relative importance of leading axes of natural climate variability documented by previous studies (Bond et al. 2003, Di Lorenzo et al. 2008, Yeh et al. 2011). Such non-stationary patterns of community-level biological variability are conceptually similar to the idea of novel community combinations under different climates (Parmesan et al. 2005), and they represent a rarely-considered challenge for scenarios of ecological response to future climate states.

The underlying dynamics for basin-scale climate-biology covariation are population-specific responses to basin-scale propagation of climate signals through teleconnections (Schwing et al. 2010). Community-level variability arises both through responses to climate variability that are synchronous across populations and species (Wilderbuer et al. 2002, Mueter et al. 2007), as well as species interactions (e.g., predation, competition) that are sensitive to climate (Litzow and Ciannelli 2007, Poloczanska et al. 2008). However, understanding of the mechanisms by which climate variability regulates individual populations in our study region is incomplete (Mueter et al. 2007), and such an understanding is made more difficult by the expectation that these mechanisms may be nonstationary over space and time (Mueter et al. 2002, Ciannelli et al. 2004, Litzow and Ciannelli 2007). Furthermore, community-level responses are subject to the complex dynamics that arise when individual population-level responses are compiled (Drake 1991), and mechanistic understanding of community-level variability is currently beyond our reach. Climate-biology covariation at large spatial scales is therefore studied with the indicator approach that we use here, which contributes to a phenomenological understanding based on the observation of past events (e.g., deYoung et al. 2004b, deYoung et al. 2008, Möllmann and Diekmann 2012). Although the PDO pattern is believed to have been established for centuries (Gedalof et al. 2002) only one ecologically strong PDO shift (1976/77) and one ecologically weak shift (1988/89) have occurred during the period for which community-wide biological data are available. With such a small population of past events to compare to, our understanding remains highly subject to event-by-event variability and surprises, and these limitations to our understanding become particularly clear when we are confronted with an event of potential

significance in both climate and biology, such as the putative 2007/08 shift in the PDO and NPGO (Fig. 2.8a).

Observation of past climate regime shifts led to interest in developing methods for early recognition of climate regime shifts as they occurred (e.g., with STARS, Rodionov 2006). However, in spite of the strong decadal-scale variability in climate indices such as the PDO, there is also considerable interannual variability, and the recognition of statistically significant departures from past values is no guarantee of stability in a new climate state, particularly when climate regime shifts are understood as the result of red noise processes (Bond et al. 2003, Peterson and Schwing 2003, Litzow 2006). As such, our "pulse-press" approach is merely a way to formalize the need for adequate observation that has always existed when assessing putative shifts.

Although the putative 2007/08 shift currently appears to have been large enough, and persistent enough, to be ecologically important, available data do not support the hypothesis of widespread ecological response to this event. On one hand, the PDO-negative, NPGO-positive conditions that have existed since the shift (Fig. 8a) are consistent with the simultaneous change in both indices that is associated with ecologically-important climate regime shifts (Di Lorenzo et al. 2008), and the persistent press perturbation following the 2007/08 event appears similar to that following the ecologically-important 1976/77 shift (Fig. 2.8b). Furthermore, the 2007/08 change in $PC1_{biol}$-$PC2_{biol}$ phase space was by far the largest in the record for the full set of biology time series (Fig. 2.6), which is strongly suggestive of an incipient large-scale biological response to the PDO/NPGO shift. However, the subset of biology time series that could be updated at least through 2010 do not show evidence of persistent change: neither $PC1_{biol}$ (Fig. 2.7a) nor $PC2_{biol}$ (Fig. 2.7b) calculated from the partial data set show evidence of an abrupt change in mean values during 2008-2011. Because most of the Hare and Mantua (2000) biology parameters are lagged (to cohort strength at age-0 or year of ocean entry), an immediate, or short-lag, response to climate variability is expected, and available biological data do not show such a response to the 2007/08 shift. While we made every effort to ensure data quality at the end of time series by, for instance, removing recent model-derived recruitment estimates that have not yet been empirically evaluated, we caution that there may be sources of variability towards the ends of biological time series of which we are unaware, and more years of observation will be needed before we are certain that our evaluation of post-2007/08 community variability is not to some degree an

artefact of our data. Additionally, non-linear behavior consistent with alternative stable states has been demonstrated for several populations in the region (Hsieh et al. 2005, Hsieh and Ohman 2006). While alternate stable state dynamics have not been demonstrated for community-level biological variability at the scale of the northeast Pacific, such complex behavior would suggest the possibility of both hysteresis (i.e., resilience to reversibility of the ecological consequences of the 1976/77 PDO switch) and/or a sudden ecological response, at an unknown threshold, to ongoing PDO-negative, NPGO-positive forcing (Scheffer et al. 2001). Both possibilities suggest that ecological response to a climate regime shift need not be immediate and may be gradual, as in the case of past $PC1_{biol}$ variability. A key question for continued monitoring for possible ecological consequences of the 2007/08 event therefore becomes whether the remarkable stability in the PDO and NPGO Indices over recent years (Fig. 2.8) will continue. La Niña conditions are often associated with negative PDO values (Yeh et al. 2011), and the tropical Pacific has experienced three Niña winters and one Niño winter since 2007 (Bjorkstedt et al. 2011; www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml). Accordingly, an important indication of the persistence of the recent PDO-negative state will come with the next reversion to El Niño conditions.

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Supporting Information

Table 2.S1. Description and sources for time series used in analysis. All time series values that span two calendar values are assigned to the year corresponding to January. CI = climate index, CP = climate parameter, I = macroinvertebrate condition or abundance, G = groundfish recruitment, P = small pelagic fish catch or recruitment, S = salmon catch or migration behavior, Z = zooplankton phenology or abundance. "H&M" refers to Hare and Mantua (2000). Scientific names are given for the first occurrence of each taxon.

Name	Code	Type	Description	Source for update	n (years)
North Pacific Atmospheric Index	NPATMOS	CI	Average of PNA (DJF), NPI (DJF), ALPI (DJFM), all standardized as mean = 0, unit variance. Sign of NPI reversed. ALPI only available for 1965-2008, so 2009-10 estimated with regression: NPATMOS = 0.9763*((PNA+NPI)/2) + 0.0079, r^2 = 0.972	climatedataguide.ucar.edu; jisao.washington.edu; www.pac.dfo-mpo.gc.ca	46
Pacific Decadal Oscillation - winter index	PDOWIN	CI	DJF mean standardized values for the PDO index, derived as the leading PC of monthly SST anomalies in the North Pacific Ocean, poleward of 20º N	jisao.washington.edu	47
Pacific Decadal Oscillation - summer index	PDOSUM	CI	JJA mean standardized values for the PDO index, derived as the leading PC of monthly SST anomalies in the North Pacific Ocean, poleward of 20º N	jisao.washington.edu	47
North Pacific Gyre Oscillation – winter index	NPGOWIN	CI	DJF mean values for the NPGO index, derived as the leading PC of monthly SSHa anomalies in the North Pacific Ocean, poleward of 25º N	o3d.org/npgo	47
North Pacific Gyre Oscillation – summer index	NPGOSUM	CI	JJA mean values for the NPGO index, derived as the leading PC of monthly SSHa anomalies in the North Pacific Ocean, poleward of 25º N	o3d.org/npgo	47
Southern Oscillation index	SOI	CI	DJF average monthly difference (T-D) between mean sea level pressure anomalies at Tahiti (T) and Darwin (D)	www.cgd.ucar.edu	47
ENSO 3.4 - winter index	ENSOWIN	CI	DJF mean East Central Tropical Pacific SST (5º N - 5º S, 170º W - 120º W)	www.esrl.noaa.gov	47

Name	Code	Type	Description	Source for update	n (years)
ENSO 3.4 - summer index	ENSOSUM	CI	JJA East Central Tropical Pacific SST (5º N - 5º S, 170º W - 120º W)	www.esrl.noaa.gov	47
Arctic Oscillation index	AO	CI	JFM mean monthly values of index values constructed by projecting the daily (00Z) 1000mb height anomalies poleward of 20°N onto the loading pattern of the AO	www.cpc.noaa.gov	47
King Salmon air temperature	KSAT	CP	DJF average of monthly mean air temperature	climate.gi.alaska.edu	46
Cold Bay air temperature	CBAT	CP	DJF average of monthly mean air temperature	climate.gi.alaska.edu	46
Kuskokwim stream flow	KUSSTR	CP	Sum of Sept.-Oct. monthly mean flow values	waterdata.usgs.gov	46
St. Paul Island sea surface temperature	PISST	CP	DJF mean temperature at 56º-58ºN, 176º-172ºW from ERSST	lwf.ncdc.noaa.gov	46
Bering Sea ice cover index	BSICE	CP	Winter ice cover - combines old (1954-2006) and new (1979-2010) indices from NOAA PMEL: new = 0.902*old + 0.1324, $r^2 = 0.592$	www.beringclimate.noaa.gov	47
Eastern Bering Sea jellyfish biomass	BSJELLY	I	Biomass of large medusae (Scyphozoa) from NOAA summer trawl survey. Pre-1982 data calculated from H&M data using formula: new data = 0.2001*H&M data + 0.1985,$r^2 = 1$	access.afsc.noaa.gov	34
Eastern Bering Sea pollock recruitment	EBSPOLL	G	Recruitment of age-1 *Theragra chalcogramma* by year class, log transformed	www.fakr.noaa.gov	44
Eastern Bering Sea Pacific cod recruitment	EBSCOD	G	Recruitment of age-0 *Gadus macrocephalus* by year class, log transformed	www.fakr.noaa.gov	36
Eastern Bering Sea yellowfin sole recruitment	EBSYFS	G	Recruitment of age-5 *Limanda aspera* by year class, log transformed	www.fakr.noaa.gov	40

Name	Code	Type	Description	Source for update	n (years)
Eastern Bering Sea Greenland turbot recruitment	EBSTRBT	G	Recruitment of age-0 *Reinhardtius hippoglossoides*, log-transformed. Current model combines Aleutian Islands and Eastern Bering Sea populations	www.fakr.noaa.gov; Jim Ianelli, NOAA, pers. comm.	41
Eastern Bering Sea arrowtooth flounder recruitment	EBSATF	G	Recruitment of age-1 *Atheresthes stomias* by year class, log transformed. 1974 value estimated from previous (i.e., 2010) stock assessment: current assessment = old assessment* 0.9777 + 0.2204, $r^2 = 0.976$	www.fakr.noaa.gov	34
Eastern Bering Sea rock sole recruitment	EBSRSOLE	G	Recruitment of age-4 *Lepidopsetta* spp. by year class, log transformed	www.fakr.noaa.gov	35
Eastern Bering Sea flathead sole recruitment	EBSFSOLE	G	Recruitment of age-3 *Hippoglossoides elassodon* by year class, log transformed	www.fakr.noaa.gov	34
Eastern Bering Sea Alaska plaice recruitment	EBSAKPLA	G	Recruitment of age-3 *Pleuronectes quadrituberculatus* by year class, log transformed	www.fakr.noaa.gov	34
Eastern Bering Sea herring recruitment	EBSHERR	P	Recruitment of age-4 *Clupea pallasii* in Togiak district, log-transformed. 1973 value estimated from previous (2010) assessment: current assessment = old assessment*0.9906 + 0.1077, $r^2 = 0.976$	access.afsc.noaa.gov; Greg Buck, ADF&G, pers. comm.	34
Aleutian Islands Atka mackerel recruitment	AIATKA	G	Recruitment of age-1 *Pleurogrammus monopterygius* by year class, log transformed, combined for Eastern Bering Sea and Aleutian Islands. 1975 value estimated from H&M data: current model = 0.2128*(H&M) + 2.5902, $r^2 = 0.65$	www.fakr.noaa.gov	32
Aleutian Islands Pacific ocean perch recruitment	AIPOP	G	Recruitment of age-3 *Sebastes alutus* by year class, log-transformed	www.fakr.noaa.gov; Paul Spencer, NOAA, pers. comm.	31

Name	Code	Type	Description	Source for update	n (years)
Western Alaska chinook salmon catch	WAK_CH	S	Commercial catch of *Oncorhynchus tsawytscha* in Bristol Bay, Peninsula and Arctic-Yukon-Kuskokwim management areas, log-transformed and lagged 3 years	www.cf.adfg.state.ak.us; Doug Eggers, ADF&G, pers. comm.	44
Western Alaska chum salmon catch	WAK_CM	S	Commercial catch of *O. keta* in Bristol Bay, Peninsula and Arctic-Yukon-Kuskokwim management areas, log-transformed and lagged 3 years	www.cf.adfg.state.ak.us; Doug Eggers, ADF&G, pers. comm.	44
Western Alaska coho salmon catch	WAK_CO	S	Commercial catch of *O. kisutch* in Bristol Bay, Peninsula and Arctic-Yukon-Kuskokwim management areas, log-transformed and lagged 1 year	www.cf.adfg.state.ak.us; Doug Eggers, ADF&G, pers. comm.	46
Western Alaska pink salmon catch	WAK_PI	S	Commercial catch of *O. gorbuscha* in Bristol Bay, Peninsula and Arctic-Yukon-Kuskokwim management areas, log-transformed and lagged 1 year	www.cf.adfg.state.ak.us; Doug Eggers, ADF&G, pers. comm.	46
Western Alaska sockeye salmon catch	WAK_SO	S	Commercial catch of *O. nerka* in Bristol Bay, Peninsula and Arctic-Yukon-Kuskokwim management areas, log-transformed and lagged 2 years	www.cf.adfg.state.ak.us; Doug Eggers, ADF&G, pers. comm.	45
East Pacific / North Pacific teleconnection index	EP/NP	CI	JF mean of monthly mean index values calculated from 500 mb height anomaly data. Data multiplied by -1 to match sign in H&M data	www.cpc.ncep.noaa.gov	47
Kodiak air temperature	KODAT	CP	DJF average of monthly mean air temperature	climate.gi.alaska.edu	46
Kenai River stream flow	KENSTR	CP	Sum of Sept.-Oct. monthly mean flow values	waterdata.usgs.gov	46
Ocean Station Papa trajectory index	PAPA	CP	Endpoint latitude for OSCURS (Ocean Surface Current Simulator) model run 90 days beginning at 50º N 145º W on Dec. 1 of the year before labeled year	las.pfeg.noaa.gov	47
GAK1 sea surface temperature	GAK1SST	CP	DJF mean GAK1 temperature at 0 m depth	ims.uaf.edu	31

Name	Code	Type	Description	Source for update	n (years)
Upwelling intensity at 60N, 149W	U60N149W	CP	MAMJJA average of monthly upwelling intensity values	www.pfeg.noaa.gov	47
Upwelling intensity at 57N, 137W	U57N137W	CP	MAMJJA average of monthly upwelling intensity values	www.pfeg.noaa.gov	47
East Pacific zooplankton phenology	EPZOO	Z	Date of *Neocalanus plumchrus* peak biomass at Ocean Station Papa (Julian day). 1965-1980 estimated by biomass, 1981-2004 estimated by stage ratio. Two methods treated as interchangeable, though error introduced by combining the two cannot be estimated. Additionally, 1985, 1990, 1999 and 2006-2011 estimated with continental margin data, using the relationship: gyre date = 0.8177*continental date + 49.834, n = 12 years, r^2 = 0.770. Seven other missing years estimated from PC1 of abundance of 3 leading taxa in SCVI: gyre phenology = 2.1982*PC1^2 - 9.7026*PC1 +141.6, n = 14 years, r^2 = 0.578	Mackas et al. 2007, D. Mackas, DFO, pers. comm.	46
Gulf of Alaska shrimp catch	GOASHR	I	Proportion (by weight) of shrimp (Pandalidae) in annual small-mesh survey catches	Dan Urban, NOAA, pers. comm.	39
Gulf of Alaska sablefish recruitment	GOASAB	G	Recruitment of age-2 *Anoplopoma fimbria* by year class, log transformed. Current model is for all Alaskan waters, but population is predominantly in GOA	www.fakr.noaa.gov	45
Gulf of Alaska Pacific halibut recruitment	GOAHAL	G	Recruitment of age-8 *Hippoglossus stenolepis*, log transformed. Pre-1988 values estimated from old assessment model: new model = 0.9903*old model + 0.098, r^2 = 0.825. 2005 & 2006 values estimated from age-6 abundance estimates from new model	S. Hare, IPHC, pers. comm.	41

Name	Code	Type	Description	Source for update	n (years)
Gulf of Alaska Pacific Ocean perch recruitment	GOAPOP	G	Recruitment of age-2 Pacific Ocean perch by year class, log-transformed	www.fakr.noaa.gov	34
Gulf of Alaska pollock recruitment	GOAPOLL	G	Recruitment of age-2 walleye pollock by year class, log-transformed	www.fakr.noaa.gov	44
Gulf of Alaska Pacific cod recruitment	GOACOD	G	Recruitment of age-0 Pacific cod by year class, log-transformed. "Model B" results used	www.fakr.noaa.gov; Grant Thompson, NOAA, pers. comm.	44
Gulf of Alaska arrowtooth flounder recruitment	GOAATF	G	Recruitment of age-3 arrowtooth flounder by year class, log-transformed	www.fakr.noaa.gov	40
Prince William Sound herring recruitment	PWSHERR	P	Recruitment of age-3 Pacific herring by year class, log-transformed. 1969-1976 values estimated from H&M data (current model = 0.3515*H&M + 2.2115, $r^2 = 0.94$)	access.afsc.noaa.gov; Steve Moffit, ADF&G, pers. comm.	40
Sitka herring recruitment	SITHERR	P	Recruitment of age-3 Pacific herring by year class, log-transformed. 1968-1976 values estimated from old (2007) assessment (current model = 0.9919*old model - 0.0701, $r^2 = 0.795$)	Sherri Dressel, ADF&G, pers. comm,	41
Central Alaska chinook salmon catch	CAK_CH	S	Commercial catch in Chignik, Kodiak, Cook Inlet, Prince William Sound management areas, log-transformed and lagged 3 years	www.cf.adfg.state.ak.us; Doug Eggers, ADF&G, pers. comm.	44
Central Alaska chum salmon catch	CAK_CM	S	Commercial catch in Chignik, Kodiak, Cook Inlet, Prince William Sound management areas, log-transformed and lagged 3 years	www.cf.adfg.state.ak.us; Doug Eggers, ADF&G, pers. comm.	44
Central Alaska coho salmon catch	CAK_CO	S	Commercial catch in Chignik, Kodiak, Cook Inlet, Prince William Sound management areas, log-transformed and lagged 1 year	www.cf.adfg.state.ak.us; Doug Eggers, ADF&G, pers. comm.	46

Name	Code	Type	Description	Source for update	n (years)
Central Alaska pink salmon catch	CAK_PI	S	Commercial catch in Chignik, Kodiak, Cook Inlet, Prince William Sound management areas, log-transformed and lagged 1 year	www.cf.adfg.state.ak.us; Doug Eggers, ADF&G, pers. comm.	46
Central Alaska sockeye salmon catch	CAK_SO	S	Commercial catch in Chignik, Kodiak, Cook Inlet, Prince William Sound management areas, log-transformed and lagged 2 years	www.cf.adfg.state.ak.us; Doug Eggers, ADF&G, pers. comm.	45
Southeast Alaska chinook salmon catch	SAK_CH	S	Commercial catch in Southeast and Yakutat management areas, log-transformed and lagged 3 years	www.cf.adfg.state.ak.us; Doug Eggers, ADF&G, pers. comm.	44
Southeast Alaska chum salmon catch	SAK_CM	S	Commercial catch in Southeast and Yakutat management areas, log-transformed and lagged 3 years	www.cf.adfg.state.ak.us; Doug Eggers, ADF&G, pers. comm.	44
Southeast Alaska coho salmon catch	SAK_CO	S	Commercial catch in Southeast and Yakutat management areas, log-transformed and lagged 1 year	www.cf.adfg.state.ak.us; Doug Eggers, ADF&G, pers. comm.	46
Southeast Alaska pink salmon catch	SAK_PI	S	Commercial catch in Southeast and Yakutat management areas, log-transformed and lagged 1 year	www.cf.adfg.state.ak.us; Doug Eggers, ADF&G, pers. comm.	46
Southeast Alaska sockeye salmon catch	SAK_SO	S	Commercial catch in Southeast and Yakutat management areas, log-transformed and lagged 2 years	www.cf.adfg.state.ak.us; Doug Eggers, ADF&G, pers. comm.	45
Skeena River stream flow	SKEESTR	CP	Sum of Oct.-Sept. monthly mean flow values at Environment Canada Usk gauge station	www.ec.gc.ca	46
Kains Island sea surface temperature	KISST	CP	DJF average of mean monthly SST at Kains Island lighthouse, BC	www.pac.dfo-mpo.gc.ca	47
Upwelling intensity at 51N, 131W	U51N131W	CP	MAMJJA average of monthly upwelling intensity values	www.pfeg.noaa.gov	47
Northern diversion rate	NDR	S	Proportion of Fraser River sockeye returning via Johnstone Strait	Michael Folkes, DFO, pers. comm.	47

Name	Code	Type	Description	Source for update	n (years)
British Columbia chinook salmon catch	BC_CH	S	Commercial catch, log-transformed and lagged 3 years	www.pac.dfo-mpo.gc.ca	44
British Columbia chum salmon catch	BC_CM	S	Commercial catch, log-transformed and lagged 3 years	www.pac.dfo-mpo.gc.ca	44
British Columbia coho salmon catch	BC_CO	S	Commercial catch, log-transformed and lagged 1 year	www.pac.dfo-mpo.gc.ca	46
British Columbia pink salmon catch	BC_PI	S	Commercial catch, log-transformed and lagged 1 year	www.pac.dfo-mpo.gc.ca	46
British Columbia sockeye salmon catch	BC_SO	S	Commercial catch, log-transformed and lagged 2 years	www.pac.dfo-mpo.gc.ca	45
British Columbia shrimp survey catch	BC_SHR	I	Estimated log-transformed biomass of *Pandalus jordani* averaged among PFMA areas 124 & 125. For 2 years when only area 124 was sampled, mean value was estimated as mean log abundance = log(area 124)*0.8046 + 1.2656, $r^2 = 0.809$	Ian Perry, DFO, pers. comm. Data maintained by Jim Boutillier, Brenda Waddell and Ian Perry (DFO, Pacific Biological Station, Nanaimo)	33
British Columbia herring recruitment	BC_HERR	P	Total estimated age-2 recruitment for five major Pacific herring stocks, log-transformed and lagged to year class	http://www.pac.dfo-mpo.gc.ca/science/species-especes/pelagic-pelagique/herring-hareng-eng.htm	42
Forks, Washington air temperature	FORAT	CP	DJF mean air temperature	cdiac.ornl.gov	47
Newport, Oregon air temperature	NEWAT	CP	DJF mean air temperature	cdiac.ornl.gov	47

Name	Code	Type	Description	Source for update	n (years)
Eureka, California air temperature	EURAT	CP	DJF mean air temperature	cdiac.ornl.gov	47
Columbia River stream flow	COLSTR	CP	Sum of Sept.-Oct. mean flow at USGS gauge station at the Dalles, OR	waterdata.usgs.gov	47
Eight Rivers runoff index	8RIVSTR	CP	Sum of total monthly flow for Oct.-Jul. for 4 rivers in Sacramento drainage and 4 rivers in San Joaquin drainage	cdec.water.ca.gov	47
Scripps pier sea surface temperature	SCRSST	CP	DJF mean SST at Scripps Pier, CA	Melissa Carter, UCSD, pers. comm. Data from Shore Stations Program with current support from the California Department of Boating and Waterways	47
Upwelling intensity at 48N, 125W	U48N125W	CP	MAMJJA average of monthly upwelling intensity values	www.pfeg.noaa.gov	47
Upwelling intensity at 42N, 125W	U42N125W	CP	MAMJJA average of monthly upwelling intensity values	www.pfeg.noaa.gov	47
Upwelling intensity at 36N, 122W	U36N122W	CP	MAMJJA average of monthly upwelling intensity values	www.pfeg.noaa.gov	47
California current zooplankton abundance	CCZOO	Z	JJA mean total zooplankton biomass from CalCOFI lines 80-93, log-transformed	Amy Hays, NOAA, pers. comm.	35
Oyster condition index	OCI	I	Index of meat:shell ratio for Pacific oysters (*Crassotrea gigas*) from four sites (Stackpole, Stony Pt., Parcel A, Oysterville) in Willapa Bay	Bruce Kauffman, WDFW, pers. comm.	47

Name	Code	Type	Description	Source for update	n (years)
West coast Pacific mackerel recruitment	WCMACK	P	Recruitment of age-0 *Scomber japonicus* off southern California and Mexico, log-transformed. Estimates are by "fishing year" (July-June), these were lagged one year to achieve consistency with other variables (mostly climate) that span years, i.e., to the year corresponding to January. 1965-1983 values estimated from previous (2009) assessment with relationship current assessment = 0.8387*(old assessment) + 0.9632, $r^2 = 0.825$	www.pcouncil.org; Paul Crone, NOAA, pers. comm.	45
West coast sablefish recruitment	WCSAB	G	Recruitment of age-0 sablefish by year class, log-transformed	www.pcouncil.org	32
West coast Dover sole recruitment	WCDSOLE	G	Recruitment of age-0 *Microstomus pacificus*, log-transformed	www.pcouncil.org	32
West coast widow rockfish recruitment	WCWIDOW	G	Recruitment of age-3 *Sebastes entomelas* by year class, log-transformed	www.pcouncil.org	40
West coast chilipepper rockfish recruitment	WCCHILI	G	Recruitment of age-0 *Sebastes goodei* by year class, log-transformed	www.pcouncil.org	40
West coast bocaccio recruitment	WCBOCACC	G	Recruitment of age-0 *Sebastes paucispinis* recruitment off California by year class, log-transformed	www.pcouncil.org	38
West coast canary rockfish recruitment	WCCANARY	G	Recruitment of age-0 *Sebastes pinniger*, log-transformed	www.pcouncil.org	34
West coast Pacific hake recruitment	WCHAKE	G	Log-transformed median recruitment of age-0 *Merluccius productus* off British Columbia and U.S. West Coast	www.pcouncil.org	40

Name	Code	Type	Description	Source for update	n (years)
West coast sardine catch	WCSARD	P	West coast *Sardinops sagax* catches, log-transformed and lagged 4 years, to correspond with dominant 4 year old age class in fishery. Catch for 2004-2006 age classes estimated with log-transformed recruitment estimated from "update" model: catch = -0.5388*Recruitment^2 + 4.4054*Recruitment - 4.1272, r^2 = 0.87	www.pcouncil.org	42
West coast Pacific Ocean perch recruitment	WCPOP	G	Recruitment of age-3 Pacific Ocean perch off Washington and Oregon by year class, log-transformed	www.pcouncil.org	41
Washington chinook salmon catch	WA_CH	S	Commercial catch, log-transformed and lagged 3 years	www.st.nmfs.noaa.gov	43
Washington chum salmon catch	WA_CM	S	Commercial catch, log-transformed and lagged 3 years	www.st.nmfs.noaa.gov	43
Washington coho salmon catch	WA_CO	S	Commercial catch, log-transformed and lagged 1 year	www.st.nmfs.noaa.gov	45
Washington sockeye salmon catch	WA_SO	S	Commercial catch, log-transformed and lagged 2 years	www.st.nmfs.noaa.gov	44
Oregon chinook salmon catch	OR_CH	S	Commercial catch, log-transformed and lagged 3 years	www.st.nmfs.noaa.gov; www.dfw.state.or.us	43
Oregon coho salmon catch	OR_CO	S	Commercial catch, log-transformed and lagged 1 year	www.st.nmfs.noaa.gov; www.dfw.state.or.us	45
California chinook salmon catch	CA_CH	S	Commercial catch, log-transformed and lagged 3 years	www.st.nmfs.noaa.gov	43

Table 2.S2. Loadings for PCA of large-scale climate index time series.

Time series	PC1
SOI	-0.491
NPGOSUM	-0.329
NPGOWIN	-0.247
AO	-0.137
ENSOSUM	0.115
EP.NP	0.264
NPATMOS	0.336
PDOSUM	0.387
PDOWIN	0.412
ENSOWIN	0.474

Table 2.S3. Loadings for PCA of local climate parameters.

Time Series	**PC1**	**Time Series**	**PC1 (cont'd)**	**Time Series**	**PC2**	**Time Series**	**PC2 (cont'd)**
KODAT	-0.330	U48N125W	-0.033	CBAT	-0.193	U36N122W	0.153
KSAT	-0.323	KUSSTR	-0.027	KSAT	-0.161	NEWAT	0.155
KISST	-0.312	U42N125W	-0.017	KODAT	-0.144	FORAT	0.157
EURAT	-0.298	U51N131W	-0.011	COLSTR	-0.091	KENSTR	0.162
SCRSST	-0.289	U60N149W	0.013	PISST	-0.074	GAK1SST	0.194
PISST	-0.283	X8RIVSTR	0.044	SCRSST	-0.059	KUSSTR	0.275
FORAT	-0.270	U36N122W	0.056	PAPA	-0.051	U57N137W	0.302
NEWAT	-0.267	SKEESTR	0.065	SKEESTR	-0.026	U48N125W	0.324
PAPA	-0.265	U57N137W	0.066	X8RIVSTR	0.007	U60N149W	0.379
KENSTR	-0.256	BSICE	0.155	EURAT	0.032	U42N125W	0.393
CBAT	-0.226	COLSTR	0.212	BSICE	0.068	U51N131W	0.421
GAK1SST	-0.145			KISST	0.082		

Table 2.S4. Loadings for PCA of biology time series.

Time series	PC1	Time series	PC1 (cont'd)	Time series	PC2	Time series	PC2 (cont'd)
SAK_CM	-0.209	OCI	0.032	OCI	-0.219	EBSPOLL	0.072
WCSARD	-0.205	EBSFSOLE	0.032	EBSATF	-0.185	EBSFSOLE	0.073
CAK_PI	-0.195	EBSPOLL	0.034	BSJELLY	-0.139	AIPOP	0.079
SAK_CO	-0.184	WAK_CM	0.036	GOAPOP	-0.110	GOACOD	0.079
GOAHAL	-0.178	WCCHILI	0.038	EBSAKPLA	-0.109	WCDSOLE	0.096
CAK_SO	-0.175	SAK_CH	0.052	GOASHR	-0.091	WCPOP	0.099
SAK_PI	-0.168	CCZOO	0.056	SAK_CH	-0.080	BC_CH	0.099
WAK_SO	-0.160	BC_CM	0.077	GOAATF	-0.072	SAK_CO	0.100
NDR	-0.159	WCPOP	0.085	CAK_CM	-0.069	PWSHERR	0.113
CAK_CO	-0.157	EBSAKPLA	0.089	EBSYFS	-0.059	SAK_PI	0.125
GOAATF	-0.147	CA_CH	0.091	WA_CH	-0.050	CA_CH	0.136
CAK_CH	-0.136	WCWIDOW	0.093	AIATKA	-0.050	WCCANARY	0.141
WAK_PI	-0.134	BC_SO	0.099	EBSHERR	-0.048	WCWIDOW	0.148
WAK_CO	-0.128	BC_PI	0.102	EPZOO	-0.041	BC_CO	0.150
EBSATF	-0.125	WCSAB	0.110	OR_CH	-0.023	CAK_SO	0.156
CAK_CM	-0.122	EBSYFS	0.110	WCBOCACC	-0.022	EBSRSOLE	0.157
SAK_SO	-0.118	BC_SHR	0.111	WCSARD	-0.020	WAK_SO	0.161
EBSRSOLE	-0.117	PWSHERR	0.128	EBSTRBT	-0.019	WAK_PI	0.162
SITHERR	-0.094	GOAPOLL	0.129	WCHAKE	-0.018	WA_CM	0.164
BSJELLY	-0.093	WAK_CH	0.129	SAK_CM	-0.002	WA_SO	0.166
GOAPOP	-0.092	OR_CH	0.130	WCCHILI	0.009	CCZOO	0.173
WCMACK	-0.052	WCBOCACC	0.132	SITHERR	0.011	BC_PI	0.174
WA_CM	-0.048	WCCANARY	0.137	GOAHAL	0.012	WCMACK	0.177
GOACOD	-0.034	WA_SO	0.144	GOASAB	0.013	WAK_CM	0.184
AIPOP	-0.029	EBSTRBT	0.149	OR_CO	0.015	CAK_CO	0.194
AIATKA	-0.017	BC_CO	0.154	EBSCOD	0.016	BC_CM	0.197
BC_HERR	-0.015	WA_CO	0.190	BC_SHR	0.019	SAK_SO	0.211

Time series	PC1	Time series	PC1 (cont'd)	Time series	PC2	Time series	PC2 (cont'd)
GOASAB	-0.014	WA_CH	0.190	NDR	0.021	CAK_CH	0.211
WCHAKE	0.005	GOASHR	0.193	BC_HERR	0.022	WAK_CH	0.211
EBSCOD	0.007	BC_CH	0.202	GOAPOLL	0.035	BC_SO	0.223
WCDSOLE	0.011	OR_CO	0.203	CAK_PI	0.042	WAK_CO	0.231
EBSHERR	0.013	EPZOO	0.208	WA_CO	0.044	WCSAB	0.246

Chapter 3 The PDO-NPGO transition produces non-additive community control in two North Pacific ecosystems

Citation: Litzow, M.A. in review. State-dependent climate effects on community assemblages in Alaskan marine ecosystems. Submitted to *Marine Ecology Progress Series.*

Abstract

We tested competing hypotheses about the nature of ecological forcing-response relationships in the Bering Sea and Gulf of Alaska during an apparent change in relative importance between the Pacific Decadal Oscillation (PDO) and North Pacific Gyre Oscillation (NPGO) as leading modes of North Pacific internal climate variability. Our response variables were the first two PCs for 36 population time series (1965-2008) from the two ecosystems, and our forcing variables were a commercial catch time series, a regional climate trend independent of natural variability, and a set of natural climate modes. Modeling results indicated that different sets of forcing mechanisms controlled variability in both biology PCs before and after the 1988/89 PDO-NPGO switch. Biology PC1 response to the PDO and Northern Annular Mode followed different functions before and after 1988/89, while PC2 responded most strongly to commercial catch across the time series, the regional climate trend before 1988/89 and the NPGO after 1988/89. In contrast, biological response to a change in sign of the PDO in 1976/77 was best described as a phase shift, with PC1 showing a continuous (sigmoidal) response to PDO variability. Changes in forcing-response relationships for biological variability acros 1988/89 were mirrored by changes in the relative importance of the PDO and NPGO in regulating regional climate variability. Change in the leading mode of climate variability had implications for ecosystem forecasting, as predictive skill for forecasts from pre-shift observations were significantly more accurate across 1976/77 (the phase shift) than across 1988/89. Taken together, these results demonstrate a change in ecosystem control coincident to a switch in relative importance of leading modes of climate variability. Such events have important implications for "ecological surprises" and the limits of our ability to construct plausible scenarios of ecological response to future climate states.

Keywords: Bering Sea, community variability, fisheries, groundfish, Gulf of Alaska, internal climate variability, North Pacific Gyre Oscillation, Pacific Decadal Oscillation, regime shift, salmon

Introduction

Atmospheric and oceanic teleconnections produce basin-scale climate patterns that drive coherent biological variability in widely separated marine ecosystems (Schwing et al. 2010). These teleconnections in turn are subject to coherent low-frequency (decadal) temporal patterns reflecting internal climate variability (Wallace 2000). Understanding ecological responses to leading modes of natural climate variability has been a major focus of marine ecology (deYoung et al. 2008), and recognition of the ecological role of internal climate variability has provided explanations for striking basin-scale patterns in fisheries production, such as inverse regimes of salmon (*Oncorhynchus*) production between temperate and sub-Arctic ecosystems in the northeast Pacific (Mantua et al. 1997), and inverse correlations of sardine (*Sardinops*) and anchovy (*Engraulis*) populations globally (Chavez et al. 2003, Kamykowski 2012).

One potential source of ecological variability associated with natural climate modes has received little attention in the literature: switches in relative importance among orthogonal modes of climate variability. The potential importance of such changes in relative dominance among leading modes of variability is highlighted by the expectation that anthropogenic forcing of the climate may affect the strength of various modes of internal climate variability (Morgenstern et al. 2010, Bonfils and Santer 2011). This situation is best documented in the Pacific Ocean, where four of the six leading modes of global sea surface temperature (SST) variability are centered (Messié and Chavez 2011). For much of the 20th century, the Pacific Decadal Oscillation (PDO) was the leading mode of low-frequency variability in North Pacific climate (Mantua and Hare 2002), and abrupt switches in the sign of the PDO Index (first EOF/PC of detrended SST data poleward of 20°N) in the 1940s and 1970s were associated with disruption to fisheries around the Pacific (Hare and Mantua 2000, Chavez et al. 2003). However, proxy records indicate that the PDO pattern did not dominate low-frequency variability in North Pacific climate during much of the 19th century (Gedalof et al. 2002). Furthermore, an abrupt transition in internal climate dynamics in 1988/89 (Hare and Mantua 2000) apparently signaled an end, at least temporarily, to the pattern of PDO dominance that characterized much of the 20th century (Yeh et al. 2011). Following the 1988/89 event, the PDO Index lost both amplitude and autocorrelation, and began to switch sign every 1-4 years (Bond et al.

2003). At the same time, another index of natural climate variability began to show increased amplitude and autocorrelation. This mode was originally described as the "Victoria Pattern", defined as the second EOF/PC of detrended North Pacific SST (Bond et al. 2003), and was later described as the North Pacific Gyre Oscillation (NPGO), the second EOF/PC of detrended North Pacific sea surface height data (Di Lorenzo et al. 2008). Strengthening of the NPGO is mechanistically associated with the appearance of a new spatial pattern in El Niño-Southern Oscillation (ENSO) events, termed the "ENSO Modoki" (Ashok et al. 2007, Di Lorenzo et al. 2010). The incidence of ENSO Modoki increased markedly after 1990 (Yeh et al. 2009), and strengthening of ENSO Modoki and the NPGO has been attributed to anthropogenic warming (Yeh et al. 2009, Di Lorenzo et al. 2010, Messié and Chavez 2011). The NPGO is known to regulate ecological variability in the California Current and associated nearshore areas (Di Lorenzo et al. 2008, Menge et al. 2009, Cloern et al. 2010), and the NPGO pattern shows strong loadings on physical parameters across the northeast Pacific (Di Lorenzo et al. 2008), suggesting a possibility for a basin-scale biological response to increased importance of that pattern. However, the ecological consequences of the PDO-NPGO transition at basin spatial scales have not, to our knowledge, been investigated.

Ecological theory concerning non-additive forcing-response relationships provides a framework for examining the potential consequences of the PDO-NPGO transition. A central paradigm in contemporary ecology treats populations and communities as complex systems that are subject to bifurcations and sudden transitions between alternate stable states (Scheffer et al. 2001). One important prediction of alternate stable state theory is that different sets of mechanisms regulate population and community variability in different stable states (Scheffer and Carpenter 2003). Accordingly, the framework of non-additive ecosystem control that is more often used to understand changes in mean levels of external forcing variables or internal dynamics of the system (deYoung et al. 2008, Dudgeon et al. 2010, Bestelmeyer et al. 2011) also provides a framework for testing hypotheses of changing sources of ecosystem control when important drivers of the system demonstrate variability that switches among orthogonal axes.

We used a set of 36 population time series from 1965-2008 to elucidate the nature of the forcing-response relationships controlling community-level variability across two Large Marine Ecosystems (LMEs, the Bering Sea and Gulf of Alaska)

during the 1988/89 PDO-NPGO transition. Our response variables were the first two PCs for the population time series, and our forcing variables were a commercial catch time series, a regional climate trend independent of natural climate variability and a set of natural climate modes including the PDO and NPGO. To test the hypothesis that different mechanisms controlled biological variability before and after 1988/89, we used a model selection approach to evaluate three hypothetical forcing-response relationships (environmental tracking, phase shift and non-additive forcing) across the 1988/89 event. We applied the same approach to a 1976/77 change in sign of the PDO to compare forcing-response relationships during abrupt change in a single climate mode (1976/77) with a shift between orthogonal modes (1988/89). Finally, change in the leading modes of internal climate variability suggests the possibility of "ecological surprises"; situations where past understanding of ecosystem function is of little help in understanding current conditions (Doak et al. 2008). To evaluate the potential for ecological surprise in understanding climate-biology covariation over large spatial scales following a switch between leading modes of internal climate variability, we compared the ability of statistical models to accurately predict biological variability following the 1976/77 change in the PDO and the1988/89 PDO-NPGO switch.

Methods

To illustrate the switch in relative importance of the PDO and NPGO after the 1988/89 climate transition we plotted the winter (NDJFM) amplitude of the two indices during 1965-2008 (absolute value smoothed with 11-year running mean and normalized as mean 0, unit variance); similar analysis has previously been published by Yeh et al. (2011). We tested for a change in the relative importance of the two climate modes in driving climate in our study region with linear models relating PC1 for six regional climate parameters to values of the PDO and NPGO indices. The regional parameters were spring-summer (AMJJ) downwelling strength for 60ºN 149ºW, 60ºN 146ºW and 57ºN 137ºW; winter (NDJFM) SST and SLP for the combined Bering Sea and Gulf of Alaska; and the Papa Trajectory Index (PTI), the end latitude of the 90-day trajectory for a simulated drifter released at 50ºN 145ºW on December 1 of the year prior to the year of interest. Winter SLP and SST are

expected to covary with both the PDO and NPGO (Mantua and Hare 2002, Di Lorenzo et al. 2008, Yeh et al. 2011); the downwelling indices and PTI were included to reflect NPGO regulation of Gulf of Alaska wind stress and the strength and position of the Alaskan Gyre (Di Lorenzo et al. 2008). Regional SST was calculated from the ERSSTv3.b data set for a polygon with corners at 61°N 173°W, 61°N 135°W, 54°N 130°W and 54°N 173°W, and SLP was calculated from the NCEP/NCAR reanalysis for the same polygon. The PTI and upwelling index time series were obtained from www.pfeg.noaa.gov; we refer to "downwelling" throughout the paper to reflect the persistently negative values of upwelling indices in the downwelling-dominated Gulf of Alaska ecosystem (Stabeno et al. 2004).

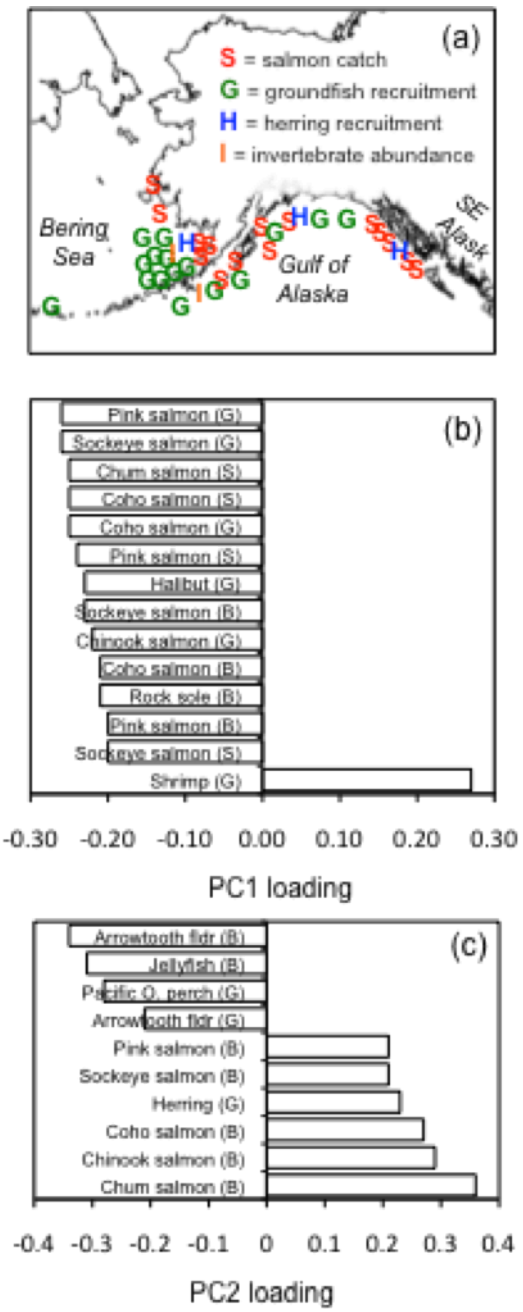

Fig. 3.1 (a) Approximate location of 36 population time series used in analysis. (b) Time series showing strongest loadings (absolute value ≥ 0.2) on biology PC1. (c) Time series showing strongest loadings on biology PC2. B = Bering Sea, G = Gulf of Alaska, S = southeast Alaska (part of the Gulf of Alaska). Redrawn from Litzow et al. (2014).

The biological data in our study are the first and second PCs for 36 populations from the Bering Sea (n = 17) and Gulf of Alaska (n = 19; Fig. 3.1a), first published for the years 1965-1997 by Hare and Mantua (2000), and updated by us for the years 1965-2008. These time series are dominated by parameters from commercially important fish populations (commercial salmon catches, recruitment estimates for groundfish and Pacific herring), all log-transformed and lagged to year of ocean entry or cohort year. Time series descriptions, sources and scientific names are presented in

Table 3.S1; for more detailed descriptions see Hare and Mantua (2000) and Litzow et al. (2014). While the original Hare and Mantua (2000) dataset included populations from Baja California to the Bering Sea, we excluded populations from the southern half of this study area from our own analysis out of concern that overfishing and anadromous habitat loss would obscure patterns of climate-biology covariation in that region (Nehlsen 1997, Levin et al. 2006). Prior to PC analysis, we estimated the 6% of time series values that were missing using multiple imputation (five iterations of 100 imputations each) with Bayesian linear regression techniques implemented in the MICE package in the computer language R (Van Buuren and Oudshoorn 1999, R Development Core Team 2010). If the CV for estimated PC scores (SD/mean from the 100 imputations in the final iteration) exceeded 1, we judged that too much uncertainty had been introduced by estimating missing values and these scores were excluded from further analysis. Biology PC1 and PC2 together explained 43.0% of total variance, more than twice the amount expected from a dataset with no correlation between variables (Jackson 1993). Biology PC1 explained 30.6% of total variance, and showed strong loadings (absolute value ≥ 0.2) on fourteen time series. Eleven salmon time series from across the study area showed negative loadings, as did Gulf of Alaska halibut and Bering Sea rock sole; Gulf of Alaska shrimp showed a positive loading (Fig. 3.1b). Biology PC2 explained 12.4% of total variance, and showed strong loadings on ten time series: negative loadings by Bering Sea arrowtooth flounder and jellyfish and Gulf of Alaska Pacific Ocean perch and arrowtooth flounder; and positive loadings by all five species of Bering Sea salmon and Prince William Sound herring (Fig. 3.1c). Complete loadings are presented in Table 3.S2. Biology PC scores from our update were well correlated with the biology PC scores from the original Hare and Mantua (2000) dataset (PC1, $r = 0.96$; PC2, $r = 0.62$).

A previous study (Litzow et al. 2014) provided us with an *a priori* set of hypothesized forcing variables that were expected to be most important for each biology PC score. Using linear analysis across the entire time series, the previous study found that variability in biology PC1 most strongly responded to the PDO, the Northern Annular Mode (NAM, the leading EOF of northern hemisphere SLP) and a regional climate trend, independent of natural modes of climate variability. Biology PC2 most strongly responded to the size of the commercial catch lagged 3 years, the NPGO, and the same regional climate trend independent of natural modes. We

obtained PDO and NAM indices from www.jisao.washington.edu, and the NPGO index from www.o3d.org. Recognizing that variability in leading modes of natural North Pacific climate variability is most coherent in winter, we used NDJFM means for the PDO and NPGO in analysis, and JFM means for the NAM.

The commercial catch time series that we used sums the total catch size from best available data for domestic and foreign fleets, including both landings, and, when available, discards (Litzow and Urban 2009). The regional climate trend used in analysis of biological forcing was obtained from Litzow et al. (2014) and consisted of residual values from the first PC of four regional climate variables (SST and SLP for the entire study region, freshwater discharge for the Gulf of Alaska and ice cover for the Bering Sea), regressed on a comprehensive set of natural climate modes (PDO, NPGO, NAM, Pacific-North America Pattern, North Pacific Index and Multivariate El Niño-Southern Oscillation Index). These residual values were significantly correlated with both year and global temperature anomalies, and we interpret them as the regional expression of anthropogenic climate change.

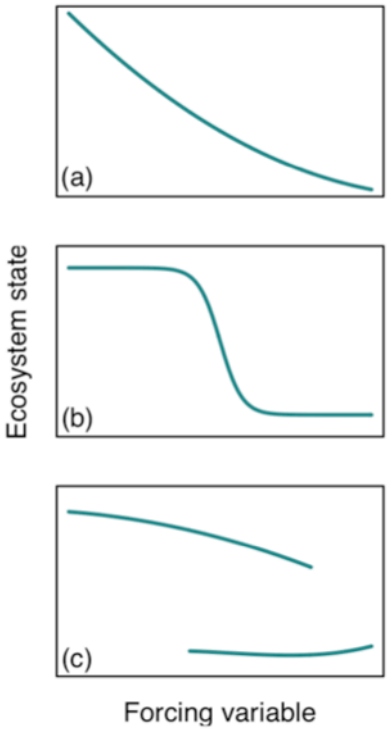

Fig. 3.2 Three hypothetical ecosystem responses to variability in external forcing parameters (e.g., fishing or climate variability). (a) Environmental tracking, corresponding to linear model or generalized additive model (GAM) with effective degrees of freedom (EDF) < ~2.5. (b) Phase shift, corresponding to GAM with EDF > ~2.5. (c) Non-additive forcing, corresponding to threshold generalized additive model (TGAM). Redrawn from Scheffer et al. (2001).

We tested three competing hypotheses that expressed forcing-response relationships as environmental tracking, phase shifts or non-additive forcing (Scheffer et al. 2001, Dudgeon et al. 2010, Bestelmeyer et al. 2011). Specifically, we used the small-sample Akaike's Information Criterion (AICc) to select between linear models or generalized additive models (GAMs) with effective degrees of freedom (EDF) < ~2.5, corresponding to gradual tracking of variable forcing conditions (Fig. 3.2a), GAMs with EDF > ~ 2.5, corresponding to abrupt phase shifts (Fig. 3.2b), and threshold generalized additive models (TGAMs), corresponding to

non-additive relationships described by separate forcing-response functions (Fig. 3.2c). The GAM approach is formulated as:

$$y_t = g_1 x1_t + g_2 x2_t + g_3 x3_t + \varepsilon_t$$

where $x1$, $x2$ and $x3$ are the three candidate explanatory variables, g_1, g_2 and g_3 are smooth functions estimated with penalized regression splines (Wood 2008), and t is the year. We limited GAM smoothing (EDF ≤ 3) to correspond with the range of response curves (linear, quadratic or sigmoidal) predicted by hypothesized forcing-response relationships (Fig. 3.2). The TGAM formulation builds on the GAM approach by fitting separate non-parametric regressions before and after a threshold year in the time series, t^*:

$$y_t = \varepsilon_t + \begin{cases} g_1 x1_t + g_2 x2_t + g_3 x3_t & \text{if } t \le t^* \\ g_4 x1_t + g_5 x2_t + g_6 x3_t & \text{if } t > t^* \end{cases}$$

We further limited smoothing in TGAMs (EDF ≤ 2) to correspond to the more linear (i.e., non-sigmoidal) forcing-response relationships predicted for separate functions under the non-additive hypothesis (Fig. 3.2c). While TGAM analysis often involves estimation of the threshold value as an additional model parameter (Ciannelli et al. 2004, Ciannelli et al. 2012), we were interested in testing hypotheses of non-additive control only across the 1976/77 and 1988/89 events, and we therefore fixed values of t^* at 1976 and 1988. Analysis for PC1 was conducted using data from 1965-1988 to assess the 1976/77 event, and data from 1977-2008 to assess the 1988/89 event. CV values for PC2 were > 1 during 1965-1972, so these years were dropped from analysis, leaving insufficient data for analysis of PC2 dynamics across the 1976/77 event. We therefore only assessed the 1988/89 event for PC2 variability, using the full set of available data (1973-2008). Both GAMs and TGAMs utilized a Gaussian distribution and identity link as implemented in R package mgcv (Wood 2008).

Because we did not have *a priori* hypotheses about the exact parameterization of different model classes, we constructed the full set of possible linear models, GAMs and TGAMs that could be built from the three candidate variables for each PC score, and selected the best model of each class using the small-sample Akaike's Information Criterion (AICc). After the best model from each class had been selected, a second round of model selection was conducted to select the overall best model for each PC score. In addition to providing a test of competing hypothesis for the nature of ecological variability across the 1976/77 and 1988/89 events, our

analysis allowed us to test hypotheses concerning changes to the set of ecologically important forcing mechanisms over time. Specifically, we predicted that the PDO would become less important for explaining biological variability after 1976/77, and that both the regional climate trend and the NPGO would become more important. We smoothed climate parameters with a 3-year running mean before analysis because we expected biological systems to respond strongly to changes in mean climate state, but to be more resilient to stochastic (interannual) variability around the mean, and because we expected the early life-history processes that dominate the time series in our study (i.e., recruitment and juvenile survival) to be most sensitive to processes occurring at lags of -1 (e.g., adult feeding, migration and spawning behavior), 0 (e.g., advection of eggs and larvae) and 1 (e.g., juvenile survival) years.

Finally, we compared the challenge for existing ecological understanding that was posed by the 1976/77 and 1988/89 events. To compare predictive skill for community-level variability we used biology PC1 as a response variable. To illustrate the potential management challenges of non-additive changes in biological control we conducted a separate analysis using Bering Sea sockeye salmon catch as a response variable; this time series was chosen because it is one of the most economically valuable fisheries in our study region. For each shift, we constructed scenarios of possible pre-shift ecological understanding consisting of nine separate GAMs for each response variable, using the PDO as an explanatory variable. Models were based on 9, 10 or 11 years of observation and observation periods that ended 1, 2, 3 or 4 years prior to the shift. For each model we calculated predictive skill for ecological variability after the shift with the root mean squared error for an out-of-sample data set consisting of the ten years following the shift of interest (i.e., 1977-1986 or 1989-1998). We tested the hypothesis that predictive skill differed between the two shifts with a mixed-effects model treating shift identity as a fixed effect and model identity as a random effect to account for non-independence of different models in each group (Pinheiro and Bates 2000).

Results

The basin-scale switch in relative importance of the PDO and NPGO following the 1988/89 climate transition was illustrated by change in the normalized amplitude of

Table 3.1 Loadings for PC1 of six regional climate parameters expected to respond strongly to the PDO and/or NPGO for periods before and after 1988/89 climate transition. Results come from separate PCA conducted on each period. Note changing patterns of correlation among loadings between periods. "Downwelling" refers to the persistently negative values of upwelling indices used in analysis.

Parameter	PC1 1965-1988 (61% of variance)	PC1 1989-2008 (41% of variance)
AMJJ downwelling at 60ºN, 149ºW	-0.46	-0.56
AMJJ downwelling at 60ºN, 146ºW	-0.47	-0.58
AMJJ downwelling at 57ºN, 137ºW	-0.42	-0.37
NDJFM SST	0.37	-0.34
NDJFM SLP	-0.38	0.26
PAPA Trajectory Index	0.33	-0.19

the two indices over 1965-2008 (Fig. 3.3a). Linear regression with the PDO and NPGO explained 53% of variance in PC1 for regional climate during 1965-1988, and 24% during 1989-2008. We used LMG scores, equivalent to partial R^2 values independent of multicollinearity (Grömping 2007) to relate the importance of the PDO and NPGO in linear regressions from the two periods. This analysis showed the PDO dominating model explanatory power prior to 1988/89, but reduced importance of the PDO, and more even explanatory power for the two indices, after 1988/89 (Fig. 3.3b). Loadings for PCA run before and after the transition also suggested that the event involved a change in relationships among regional climate parameters. Prior to 1988/89, downwelling loadings were negatively correlated with loadings for SST and the PTI and positively correlated with SLP loading; these correlations reversed sign

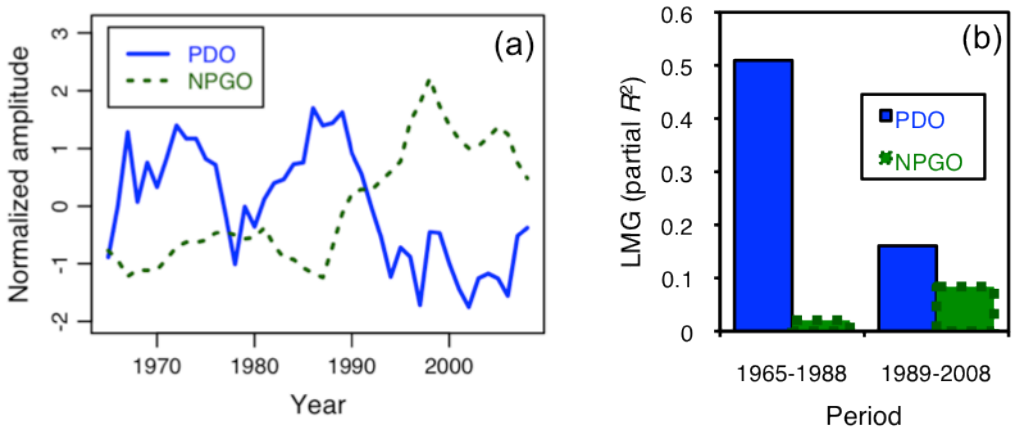

Fig. 3.3 Changes in the relative importance of the PDO and NPGO across the 1988/89 climate transition. (a) Amplitude (average absolute value) of the winter (NDJFM) PDO and NPGO indices, 1965-2008. Data smoothed with 11-year running mean and normalized as zero mean, unit variance for the period plotted. (b) Relative importance (LMG scores/partial R^2 values) for PDO and NPGO in linear regression of regional climate PC1 scores. Loadings for regional climate PCA in Table 3.1

after 1988/89 (Table 3.1).

Variability in biology PC1 scores across the 1976/77 event was best explained by a GAM invoking only the PDO (EDF = 2.86), indicating strongest support for the phase shift hypothesis (Table 3.2). The TGAM was the third-best model in this instance (Δ-AICc = 6.01), indicating poor support for non-additive forcing across this event. Biology PC1 variability across 1988/89, on the other hand, was best described by a TGAM invoking the PDO and NAM before the shift, and the PDO alone after the shift (Table 3.2). Very high Δ-AICc values (30.47 for the second-best model) indicated strong support for the non-additive hypothesis in this instance (Table 3.2). While the PDO-PC1 relationship was continuous across 1976/77, a separate function was required to describe it following 1988/89 (Fig. 3.4a). The NAM-PC1 relationship was also discontinuous between different periods (Fig. 3.4b), though the best TGAM

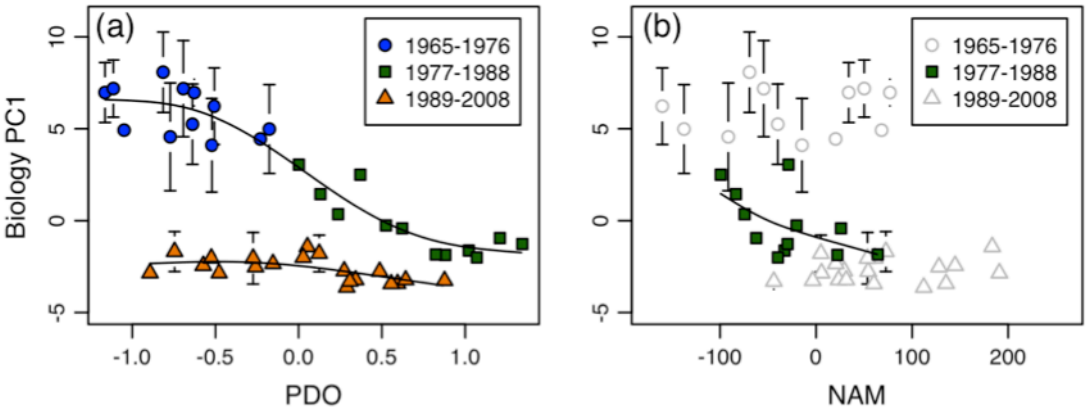

Fig. 3.4 Non-additive control of biology PC1 scores, 1965-2008: relationship with (a) the winter (NDJFM) PDO, and (b) the winter (JFM) NAM. Both climate indices smoothed with 3-year running mean prior to plotting. Filled symbols indicate years included in best models of PC1 response to external forcing (GAM for 1965-1977, TGAM for 1978-2008). Error bars ± 2SD, indicating uncertainty associated with estimating missing values.

only invoked this parameter for 1977-88 (Table 3.2).

Variability in PC2 across 1988/89 was best described by a TGAM. Large Δ-AICc values again indicated strong support for the non-additive hypothesis (Table 3.2), confirming that ecological change across the 1988/89 event was best described by a change in the set of forcing-response functions governing both axes of biological variability. Size of the commercial catch was included in the best model of biology PC2 for periods both before and after 1988/89 (Fig. 3.5a), while the climate trend was invoked only for 1973-1988 (Fig. 3.5b), and the NPGO only for 1989-2008 (Fig.

3.5c). Root mean squared prediction error was significantly higher across the PDO-NPGO transition (1988/89) than it was across the phase shift (1976/77), both for biology PC1 (t_{16} = 5.47, P = 0.0001, Fig. 3.6a), and for Bering Sea sockeye salmon catches (t_{16} = 25.29, P < 0.0001, Fig. 3.6b).

Table 3.2 Competing hypotheses for community-level transitions as environmental tracking (linear model or GAM with effective degrees of freedom [EDF] < ~2.5), phase shifts (GAM with EDF > ~2.5) or non-additive forcing (TGAM) - model selection results. Models for each class were selected from global set of models invoking all combinations of the three candidate explanatory variables for each PC, then the best model for each class was compared in a second round of model selection. "Trend" refers to trend in regional climate residuals independent of natural climate modes (Litzow et al. 2014). Values in parentheses for GAM and TGAM models are EDF values

Response	Model class	Model	R^2	AICc	Δ-AICc
PC1 1965-1988	GAM	$PC1_t = 2.83 + g_1PDO_t(2.86) + \varepsilon_t$	0.91	79.39	0
	linear	$PC1_t = 2.62 - 4.15 \cdot PDO_t - 0.01 \cdot NAM_t + \varepsilon_t$	0.90	82.23	2.85
	TGAM	$PC1_t = 1.73 + \varepsilon_t + ... g_1PDO_t(1.67)$ if $t \leq 1976$ $.... g_2PDO_t(2.27)$ if $t > 1976$	0.90	82.51	6.01
PC1 1977-2008	TGAM	$PC1_t = -1.14 + \varepsilon_t + ... g_1PDO_t(2.06) + g_2NAM_t(1.40)$ if $t \leq 1988$ $.... g_3PDO_t(2.09)$ if $t > 1988$	0.85	75.10	0
	GAM	$PC1_t = -1.75 + g_1Trend_t(1.80) + g_2NAM_t(1.90) + g_3PDO_t(1.00) + \varepsilon_t$	0.60	105.56	30.47
	linear	$PC1_t = -0.92 - 1.20 \cdot Trend_t - 0.01 \cdot NAM_t - 0.79 \cdot PDO_t + \varepsilon_t$	0.48	113.34	38.24
PC2 1973-2008	TGAM	$PC2_t = 0.49 + \varepsilon_t + ... g_1Catch_{t-3}(1.38) + g_2Trend_t(1.38)$ if $t \leq 1988$ $.... g_3Catch_{t-3}(1.38) + g_4NPGO_t(1.84)$ if $t > 1988$	0.68	121.43	0
	GAM	$PC2_t = 0.58 + g_1Catch_{t-3}(1.00) + g_2Trend_t(2.04) + g_3NPGO_t(2.84) + \varepsilon_t$	0.64	133.89	5.12
	linear	$PC2_t = 11.18 - 4.77 \cdot Catch_{t-3} - 1.04 \cdot NPGO_t + 0.01 \cdot NAM_t + 1.19 \cdot Trend + \varepsilon_t$	0.50	135.18	9.17

Discussion

The 1988/89 climate transition in the North Pacific has long been difficult to interpret; time series of climate and biology PC scores demonstrate that the shift was not a persistent change in sign of the PDO Index along the lines of those of the 1940s and 1970s (Hare and Mantua 2000), but until recently the exact nature of the event has

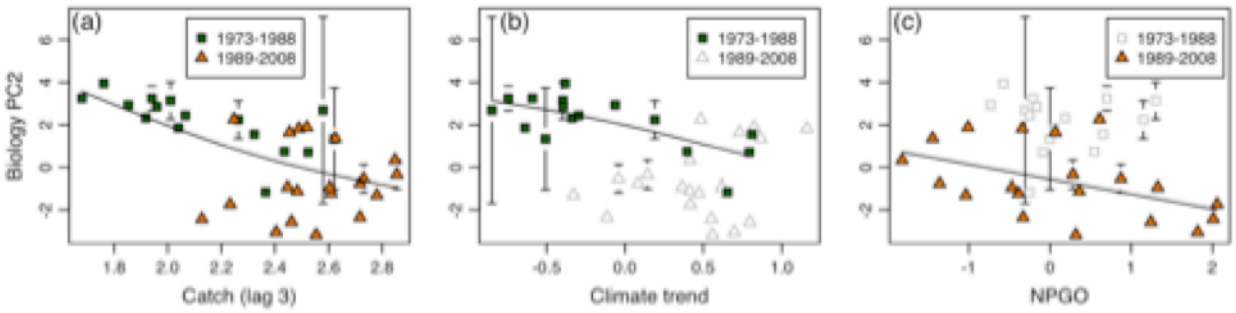

Fig. 3.5 Non-additive control of biology PC2 scores, 1973-2008: relationship with (a) commercial catch lagged 3 years, (b) the regional climate trend, independent of natural modes of climate variability, and c) the winter (NDJFM) NPGO. Filled symbols indicate years included in best model (TGAM) of PC2 response to forcing. Climate trend and NPGO smoothed with 3-year running mean prior to plotting. Error bars ± 2SD, indicating uncertainty associated with estimating missing values.

resisted definition. Along with observations of the emergence of new dominant patterns of internal climate variability (NPGO and ENSO Modoki) following 1988/89 (Fig. 3.1d; Di Lorenzo et al. 2008, Yeh et al. 2009, Messié and Chavez 2011), novel forcing-response relationships over two North Pacific LMEs (Figs. 3.3, 3.4) provide strong evidence that the PDO-NPGO transition signaled a fundamental reorganization of climate-biology covariation over large spatial scales in the North Pacific. Because forcing-response relationships on either side of the 1988/89 transition are described by independent functions (Fig. 3.4a), observations from before the transition were of limited usefulness for understanding climate-biology covariation after the transition (Fig. 3.6). Anthropogenic forcing of the climate is expected to intensify the post-1988/89 pattern of internal climate variability (Yeh et al. 2009, Di Lorenzo et al. 2010), suggesting that the change in forcing-response relationships that we demonstrate here may continue to be relevant to understanding large-scale, community-level biological variability in the North Pacific for decades. One of the greatest sources of uncertainty concerning predictions of climate responses to

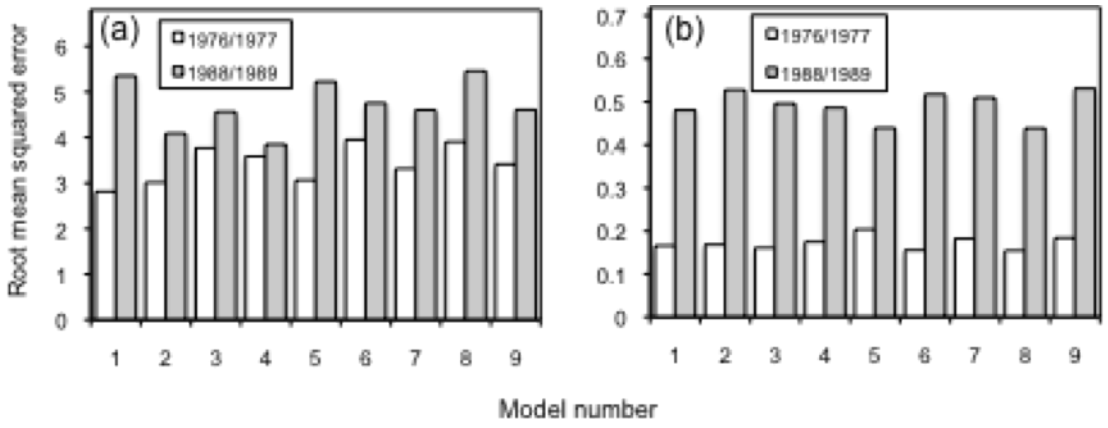

Fig. 3.6 Prediction skill for statistical models of climate-biology covariation across examples of continuous (1976/77) and non-additive (1988/89) forcing-response relationships. (a) Prediction skill for models of variability in biology PC1 scores. (b) Prediction skill for models of Bering Sea sockeye salmon catch, log transformed and lagged 2 years to reflect year of ocean entry. Models are GAMs invoking the PDO for observation periods of different lengths (9-11 years), ending 1-4 years before shifts. Mixed-effects models showed that root mean squared prediction error averaged across all models was significantly greater for non-additive forcing than for continuous forcing, both for PC1 (t_{16} = 5.47, P = 0.0001), and for Bering Sea sockeye salmon catches (t_{16} = 25.29, P < 0.0001)

continued anthropogenic forcing is the creation of previously-unobserved patterns of internal climate variability (Overland et al. 2010), and the non-additive (TGAM) approach that we use for elucidating ecological responses to the PDO-NPGO transition may be useful for understanding other transitions between orthogonal axes of climate variability.

While the 1976/77 change in sign of the PDO has often been pointed to as an example of ecological change involving alternate ecosystem states (e.g., Scheffer et al. 2001, Scheffer and Carpenter 2003), biology PC1 in our study showed a continuous, sigmoidal relationship with the PDO (Fig. 3.4a), which is inconsistent with the expectations of non-additive forcing invoked by alternate stable state theory (Scheffer and Carpenter 2003, Dudgeon et al. 2010). Our finding of a continuous relationship between the leading axis of community variability and the PDO prior to 1988/89 is supported by observations of continuous, rather than abrupt, patterns of temporal variability in biology PC1 from the entire Hare and Mantua (2000) study area (Litzow and Mueter 2014), and highlights the dangers of uncritically interpreting sudden shifts in ecological time series as evidence of alternate stable state dynamics (Dudgeon et al. 2010, Spencer et al. 2012). However, several population-level studies in the northeast Pacific show evidence of non-additive forcing or the dynamic non-

linear behavior that is characteristic of alternate stable states (Ciannelli et al. 2004, Ciannelli et al. 2005, Hsieh et al. 2005, Litzow and Ciannelli 2007), findings that are inconsistent with our community-level results.

Inconsistent results at different organizational levels are unsurprising, given the propensity of ecosystems to show different patterns at different scales (Levin 1992). The key towards resolving conflicting patterns at different scales is mechanistic understanding of the underlying dynamics (Levin 1992). Some level of mechanistic understanding for population-level climate-biology covariation has been achieved for several taxa from the region (e.g., Mueter et al. 2002, Wilderbuer et al. 2002, Litzow and Ciannelli 2007), although disentangling the mechanistic relationships of intercorrelated time series using observational data is notoriously difficult (e.g., Hunt et al. 2002, Hunt et al. 2011). Mechanistic understanding of the community-level forcing-response relationships that we document (Figs. 3.4 & 3.5) is beyond the scope of this study. However, change in the sign of correlation between the downwelling indices and other regional climate parameters (Table 3.1) does suggest that the non-additive forcing-biology relationships that we observed may be driven by non-additive change in regional climate parameters across the 1988/89 transition. And change in the PDO-regional climate relationship (Fig. 3.3b) provides an explanation for era-dependant biology PC1 responses to a range of PDO values (Fig. 3.4a); declining magnitude of the biological response to the PDO mirrors declining magnitude in the response of regional climate. In a similar vein, increased, but still weak, influence of the NPGO on regional climate post-1988/89 (Fig. 3.3b) was mirrored by increased, but still weak, influence of the NPGO on biology PC2 (Fig. 3.5c). Additionally, our observation of a non-additive relationship between biology PC1 and the NAM (Fig. 3.4b) agrees with observations of non-stationary relationships between the NAM (also known as the Arctic Oscillation) and intensity of the Aleutian Low, although the period included in the best TGAM (1977-1988) does not correspond to the post-1988/89 period of maximum amplitude in the NAM (Overland et al. 1999). Our hypothesis that the regional climate trend independent of natural variability (Litzow et al. 2014) would become more important in driving community variability in the absence of strong PDO forcing was not supported (Table 3.2). This result may reflect the need for multi-decadal time series for detecting ecological signals of anthropogenic climate change in the region, as the magnitude of the signal

of internal climate variability in regional climate parameters is several times larger than the magnitude of the residual trend (Litzow et al. 2014).

Transitions among orthogonal patterns of internal climate variability present profound difficulties for constructing realistic scenarios of future ecosystem states based on past observations. Ecological scenarios constructed for unobserved forcing conditions always involve the problem of extrapolation (Drinkwater et al. 2010); transition to a new set of ecologically important forcing mechanisms (e.g., Figs. 3.5b,c), or to a new response function for the same function (Fig. 3.4a) greatly compound the problem, as demonstrated by the deterioration of prediction skill for biological variability across the 1988/89 transition when compared to the 1976/77 PDO shift (Fig. 3.6). While the results specifically for Bering Sea sockeye salmon (Fig. 3.6b) are redundant to those for biology PC1 (Fig. 3.6a), they do illustrate the nature of particular management challenges that embed within the patterns of community-level variability that are our focus. Transitions among orthogonal axes of internal climate variability are a potential source for "black swans" – previously unobserved phenomena – with ongoing anthropogenic forcing of the climate (Overland et al. 2010, Messié and Chavez 2011). Our finding of non-additive community forcing across one such event underscores the attendant potential for discontinuities in ecological understanding.

Acknowledgements

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Supplemental Information

Table 3.S1 Biology time series included in study.

Code	Name	Scientific name	Source	Count (years)
BSJELLY	Eastern Bering Sea jellyfish biomass	Scyphozoa	www.access.afsc.noaa.gov/reem/EcoWeb/EcoChaptDataMainFrame.htm	31
EBSPOLL	Eastern Bering Sea pollock recruitment	*Theragra chalchogramma*	http://www.fakr.noaa.gov/npfmc/resources-publications/safe-reports.html	44
EBSCOD	Eastern Bering Sea Pacific cod recruitment	*Gadus macrocephalus*	http://www.fakr.noaa.gov/npfmc/resources-publications/safe-reports.html	35
EBSYFS	Eastern Bering Sea yellowfin sole recruitment	*Limanda aspera*	http://www.fakr.noaa.gov/npfmc/resources-publications/safe-reports.html	40
EBSTRBT	Eastern Bering Sea Greenland turbot recruitment	*Reinhardtius hippoglossoides*	http://www.fakr.noaa.gov/npfmc/resources-publications/safe-reports.html	39
EBSATF	Eastern Bering Sea arrowtooth flounder recruitment	*Atheresthes stomias*	http://www.fakr.noaa.gov/npfmc/resources-publications/safe-reports.html	34
EBSRSOLE	Eastern Bering Sea rock sole recruitment	*Lepidopsetta* spp.	http://www.fakr.noaa.gov/npfmc/resources-publications/safe-reports.html	35
EBSFSOLE	Eastern Bering Sea flathead sole recruitment	*Hippoglossoides elassodon*	http://www.fakr.noaa.gov/npfmc/resources-publications/safe-reports.html	34
EBSAKPLA	Eastern Bering Sea Alaska Plaice recruitment	*Pleuronectes quadrituberculatus*	http://www.fakr.noaa.gov/npfmc/resources-publications/safe-reports.html	34
EBSHERR	Eastern Bering Sea herring recruitment	*Clupea pallasii*	G. Buck, Alaska Dept. of Fish & Game, pers. comm.	34

Code	Name	Scientific name	Source	Count (years)
AIATKA	Aleutian Islands Atka mackerel recruitment	*Pleurogrammus monopterygius*	http://www.fakr.noaa.gov/npfmc/resources-publications/safe-reports.html	32
AIPOP	Aleutian Islands Pacific Ocean perch recruitment	*Sebastes alutus*	http://www.fakr.noaa.gov/npfmc/resources-publications/safe-reports.html	31
WAK_CH	Western Alaska Chinook salmon catch	*Oncorhynchus tsawytscha*	www.cf.adfg.state.ak.us	44
WAK_CM	Western Alaska chum salmon catch	*Oncorhynchus keta*	www.cf.adfg.state.ak.us	44
WAK_CO	Western Alaska coho salmon catch	*Oncorhynchus kisutch*	www.cf.adfg.state.ak.us	44
WAK_PI	Western Alaska pink salmon catch	*Oncorhynchus gorbuscha*	www.cf.adfg.state.ak.us	44
WAK_SO	Western Alaska sockeye salmon catch	*Oncorhynchus nerka*	www.cf.adfg.state.ak.us	44
GOASHR	Gulf of Alaska shrimp catch	Pandalidae	D. Urban, National Oceanic and Atmospheric Administration, pers. comm	44
GOASAB	Gulf of Alaska sablefish recruitment	*Anoplopoma fimbria*	http://www.fakr.noaa.gov/npfmc/resources-publications/safe-reports.html	44
GOAHAL	Gulf of Alaska halibut recruitment	*Hippoglossus stenolepis*	S. Hare, International Pacific Halibut Commission, pers. comm.	43
GOAPOP	Gulf of Alaska Pacific Ocean perch recruitment	*Sebastes alutus*	http://www.fakr.noaa.gov/npfmc/resources-publications/safe-reports.html	44
GOAPOLL	Gulf of Alaska walleye pollock recruitment	*Theragra chalchogramma*	http://www.fakr.noaa.gov/npfmc/resources-publications/safe-reports.html	29
GOACOD	Gulf of Alaska Pacific cod recruitment	*Gadus macrocephalus*	http://www.fakr.noaa.gov/npfmc/resources-publications/safe-reports.html	44
GOAATF	Gulf of Alaska arrowtooth flounder recruitment	*Atheresthes stomias*	http://www.fakr.noaa.gov/npfmc/resources-publications/safe-reports.html	44

Code	Name	Scientific name	Source	Count (years)
PWSHERR	Prince William Sound herring recruitment	*Clupea pallasii*	S. Moffit, Alaska Dept. of Fish & Game, pers. comm.	43
SITHERR	Sitka herring recruitment	*Clupea pallasii*	S. Dressel, Alaska Dept. of Fish & Game, pers. comm.	37
CAK_CH	Central Alaska Chinook salmon catch	*Oncorhynchus tsawytscha*	www.cf.adfg.state.ak.us	44
CAK_CM	Central Alaska chum salmon catch	*Oncorhynchus keta*	www.cf.adfg.state.ak.us	41
CAK_CO	Central Alaska coho salmon catch	*Oncorhynchus kisutch*	www.cf.adfg.state.ak.us	34
CAK_PI	Central Alaska pink salmon catch	*Oncorhynchus gorbuscha*	www.cf.adfg.state.ak.us	44
CAK_SO	Central Alaska sockeye salmon catch	*Oncorhynchus nerka*	www.cf.adfg.state.ak.us	44
SAK_CH	Southeast Alaska Chinook salmon catch	*Oncorhynchus tsawytscha*	www.cf.adfg.state.ak.us	40
SAK_CM	Southeast Alaska chum salmon catch	*Oncorhynchus keta*	www.cf.adfg.state.ak.us	40
SAK_CO	Southeast Alaska coho salmon catch	*Oncorhynchus kisutch*	www.cf.adfg.state.ak.us	41
SAK_PI	Southeast Alaska pink salmon catch	*Oncorhynchus gorbuscha*	www.cf.adfg.state.ak.us	44
SAK_SO	Southeast Alaska sockeye salmon catch	*Oncorhynchus nerka*	www.cf.adfg.state.ak.us	44

Table S3.2 Loadings for biology PC1 and PC2, sorted in decreasing order.

PC1		**PC2**	
Time series	**Loading**	**Time series**	**Loading**
GOASHR	0.27	WAK_CM	0.36
EBSTRBT	0.19	WAK_CH	0.29
EBSYFS	0.15	WAK_CO	0.27
GOAPOLL	0.15	PWSHERR	0.23
EBSAKPLA	0.13	WAK_SO	0.21
PWSHERR	0.12	WAK_PI	0.21
WAK_CH	0.11	GOACOD	0.19
SAK_CH	0.05	CAK_CO	0.16
EBSPOLL	0.04	GOAPOLL	0.14
EBSHERR	0.03	SAK_SO	0.12
EBSCOD	0.01	CAK_CH	0.11
EBSFSOLE	0.01	EBSPOLL	0.11
WAK_CM	0.01	EBSRSOLE	0.08
GOASAB	-0.02	CAK_SO	0.08
AIATKA	-0.02	EBSTRBT	0.07
GOACOD	-0.05	GOASHR	0.07
AIPOP	-0.07	EBSCOD	0.06
BSJELLY	-0.09	EBSFSOLE	0.05
GOAPOP	-0.10	SITHERR	0.05
SITHERR	-0.12	AIPOP	0.03
EBSATF	-0.13	EBSHERR	0.02
CAK_CM	-0.13	SAK_PI	0.02
GOAATF	-0.18	EBSYFS	0.02
SAK_SO	-0.20	SAK_CO	0.01
WAK_PI	-0.20	GOASAB	0.00
EBSRSOLE	-0.21	CAK_CM	-0.01
WAK_CO	-0.21	CAK_PI	-0.01
CAK_CH	-0.22	GOAHAL	-0.06
WAK_SO	-0.23	EBSAKPLA	-0.08
GOAHAL	-0.23	SAK_CM	-0.12
SAK_PI	-0.24	SAK_CH	-0.16
CAK_CO	-0.25	AIATKA	-0.18
SAK_CO	-0.25	GOAATF	-0.21
SAK_CM	-0.25	GOAPOP	-0.28
CAK_SO	-0.26	BSJELLY	-0.31
CAK_PI	-0.26	EBSATF	-0.34

Chapter 4 Rising catch variability preceded historical fisheries collapses in Alaska

Citation: Litzow, M.A., Mueter, F.J., Urban, J.D., 2013. Rising catch variability preceded historical fisheries collapses in Alaska. *Ecological Applications*, 23, 1475-1487.

Abstract

Statistical indicators such as rising variance and rising skewness in key system parameters may provide early warning of "regime shifts" in communities and populations. However, the utility of these indicators has rarely been tested in the large, complex ecosystems that are of the most interest to managers. Crustacean fisheries in the Gulf of Alaska and Bering Sea experienced a series of collapses beginning in the 1970s, and we used spatially-resolved catch data from these fisheries to test the predictions that increasing variability and skewness would precede stock collapse. Our data set consisted of catch data from 14 fisheries (12 collapsing and two non-collapsing), spanning 278 cumulative years. Our sampling unit for analysis was the Alaska Department of Fish and Game statistical reporting area (mean *n* for individual fisheries = 42 areas, range 7-81). We found that spatial variability in catches increased prior to stock collapse: a random-effects model estimating the trend in variability across all 12 collapsing fisheries showed strong evidence of increasing variability prior to collapse. Individual trends in variability were statistically significant for only four of the 12 collapsing fisheries, suggesting that rising variability might be most effective as an indicator when information from multiple populations is available. Analyzing data across multiple fisheries allowed us to detect increasing variability 1-4 years prior to collapse, and trends in variability were significantly different for collapsing and non-collapsing fisheries. In spite of theoretical expectations, we found no evidence of pre-collapse increases in catch skewness. Further, while models generally predict that rising variability should be a transient phenomenon around collapse points, increased variability was a persistent feature of collapsed fisheries in our study. We conclude that this result is more consistent with fishing effects as the cause of increased catch variability, rather than the critical slowing down that is the driver of increased variability in regime shift models. While our results support the use of rising spatial variability as a leading indicator of regime shifts, the failure of our data to support other model-derived predictions underscores the need for empirical validation before these indicators can be used with confidence by ecosystem managers.

Key words: collapse, early warning, fisheries, indicators, management, multiple stable states, regime shift

Introduction

Anthropogenic stress has increased the global risk of ecological regime shifts – abrupt, difficult-to-reverse reorganizations stemming from multiple stable state dynamics (Folke et al. 2004). Accordingly, there is much interest in developing indicators that might give managers early warning when such a shift is imminent. A promising approach comes from modeling studies suggesting that complex systems show generic statistical behaviors as resilience declines and a regime shift becomes more likely. These generic indicators include slower recovery from perturbations and increased variability, autocorrelation and skewness (Scheffer et al. 2009). It has been proposed that these indicators should be present in many types of complex systems – ecological, social, financial, and physical (Scheffer et al. 2009) – and in ecology they have been applied to sudden transitions in both ecosystems (Carpenter and Brock 2006, Guttal and Jayaprakash 2009, Donangelo et al. 2010, Carpenter et al. 2011) and populations (Oborny et al. 2005, Takimoto 2009, Drake and Griffen 2010). While these indicators have attracted much attention, a cautionary note is sounded by the observation that many ecosystem models show no early warning signs of regime shifts (Hastings and Wysham 2010), and observations that other models show inconsistent patterns (either increases or decreases) in proposed indicators prior to shifts (Dakos et al. 2012). Additionally, regime shift indicators perform poorly in models that simulate realistic levels of ecological noise (Perretti and Munch 2012). Few empirical tests of the proposed indicators have been conducted to date, and most empirical work has by necessity taken place in laboratory microcosms or small, simple ecosystems that are amenable to experimental manipulation (e.g., Cottingham et al. 2000, Drake and Griffen 2010, Carpenter et al. 2011). As a result, the utility of these regime shift indicators in the large, complex ecosystems that are typically the concern of managers remains largely untested.

Commercial fisheries collapses are often coincident with abrupt reorganization in marine communities (e.g., Hare and Mantua 2000, Choi et al. 2004), and these events have been cited as leading examples of deleterious ecological regime shifts (e.g., Scheffer et al. 2001, Biggs et al. 2009, Carpenter et al. 2011). Better indicators of the community effects of fishing have long been sought (e.g., Duplisea and Castonguay 2006), making commercial fisheries a natural venue for testing the utility of the proposed generic regime shift indicators. Furthermore, while controlled

experimental perturbation of ecosystems at very large spatial scales (i.e., $>>10^3$ km^2) is never possible, commercial fisheries offer an opportunity to test ecological theory at these scales through unplanned experiments, since fisheries constitute anthropogenic perturbations to ecosystems, and are often meticulously detailed in catch records (Jensen et al. 2012). Tests of regime shift indicators with commercial fisheries data are therefore potentially valuable both for contributing to improved fisheries management, and for assessing the general utility of these indicators in large ecosystems.

We analyzed historical catch records to evaluate the ability of generic regime shift indicators to predict a series of collapses in Alaskan crustacean fisheries that occurred during the 1970s, 80s and 90s. These collapses occurred over very large spatial scales in the Gulf of Alaska and southeastern Bering Sea (combined shelf area ~ 6.7×10^5 km^2), and were part of basin-scale community reorganization following the 1976/77 change in sign of the Pacific Decadal Oscillation (PDO) Index (Hare and Mantua 2000). Overfishing also contributed to crustacean collapses in Alaska (Orensanz et al. 1998), and the relative importance of these two forcing mechanisms is not known for any fishery in our study. Available time series may commonly be too short for calculating meaningful trends in the temporal regime shift indicators (variance, skewness and autocorrelation) proposed by modeling studies (Guttal and Jayaprakash 2009, Dakos et al. 2010), and this was the case with the time series in our study (mean length prior to collapse = 17 years). However, spatial variability and skewness are expected to show the same early-warning behavior as temporal indicators, and are suitable for use with shorter time series (Guttal and Jayaprakash 2009, Donangelo et al. 2010), so we used spatial parameters as our candidate indicators of impending collapse. Our specific goals were to test for significant increases in spatial variability and skewness of catches prior to fisheries collapses, and to test for "false positive" signals in non-collapsing fisheries. To make inferences about the mechanisms driving the changes in spatial statistics that we observed, we also tested the model-derived prediction that observed increases in regime shift indicators would be transitory, and limited to the period around the shift (e.g., Carpenter and Brock 2006, Biggs et al. 2009, Guttal and Jayaprakash 2009). To our knowledge, this study constitutes the most extensive empirical test of regime shift indicators in an actual management context to date.

Materials and Methods

Data

The fisheries in our study included trawl fisheries for pink shrimp (*Pandalus borealis*) and pot fisheries for red king crab (*Paralithodes camtshaticus*), blue king crab (*Paralithodes platypus*), snow crab (*Chionoecetes opilio*), Tanner crab (*Chionoecetes bairdi*) and spot shrimp (*Pandalus platyceros*). These fisheries were economic mainstays in coastal Alaska during the 1960s and 1970s, when groundfish and salmon catches were below long-term mean values.

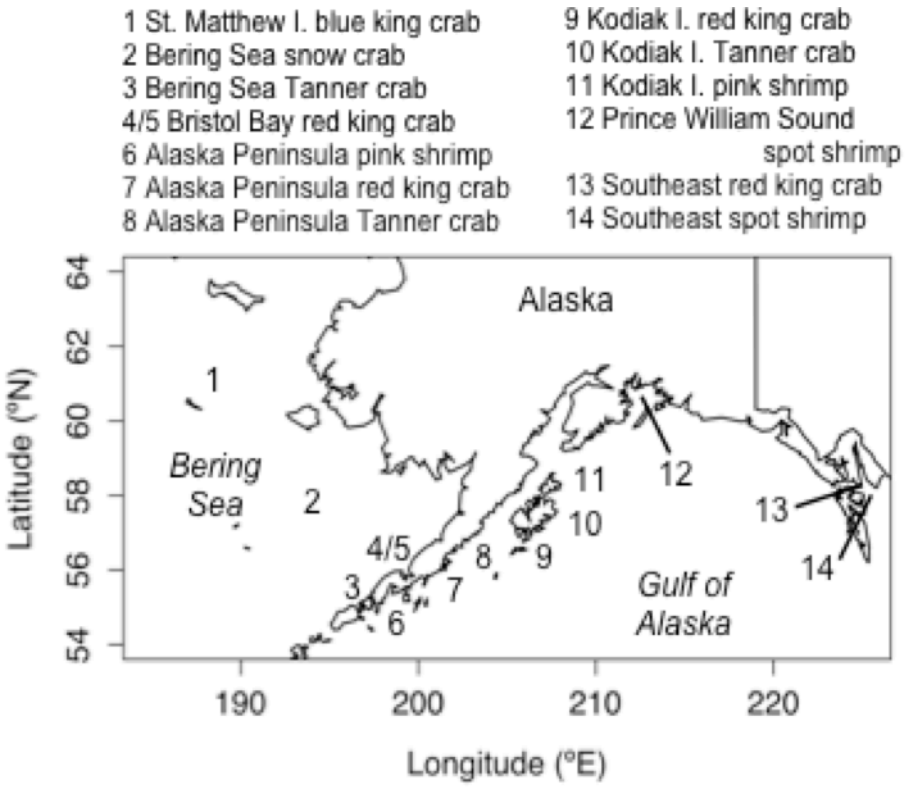


Fig. 4.1 Approximate location of fisheries included in study.

Catch records were obtained from the Alaska Department of Fish and Game (ADF&G), which has collected catch data resolved by statistical area since the late 1960s. Data from fisheries managed through limited entry or individual fishing quotas (IFQs) were excluded from analysis, as statistical parameters for these fisheries were markedly different from those of the more common derby-style fisheries. Marine ecosystem indicator time series typically require at least 10 years of data to detect a trend (Nicholson and Jennings 2004), so we limited analysis to fisheries providing a minimum of 10 years of data prior to collapse (n = 14 total fisheries, Fig.

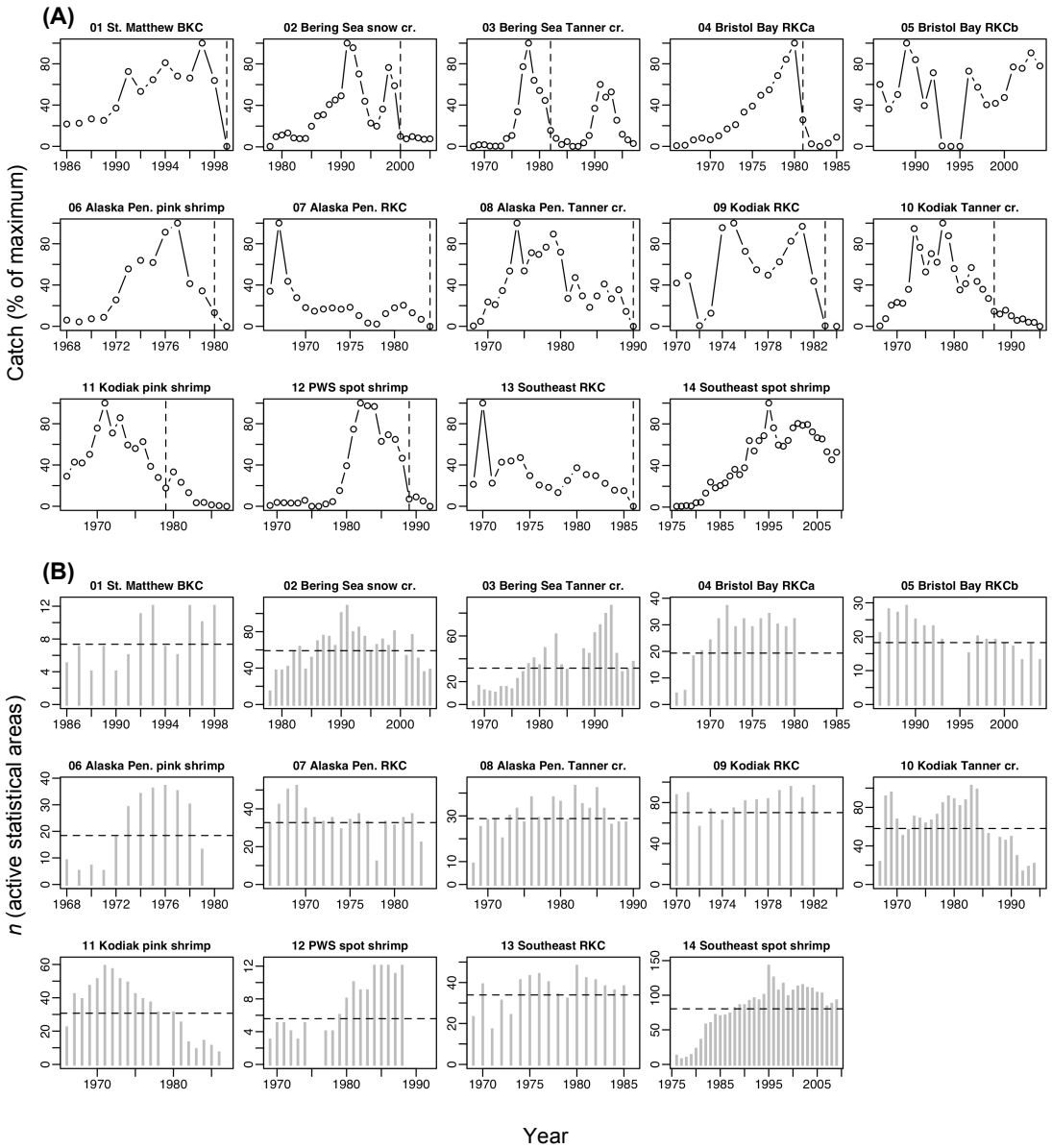
Table 4.1. Details of Alaskan crustacean fishery catch time series used in analysis.

No.	Name	Group	Scaling parameter (β)	Pre-collapse data	Post-collapse data	Mean n (areas)
1	St. Matthew I. blue king crab	collapse	2.2	1986-1998	n/a	8
2	Bering Sea snow crab	collapse	1.9	1978-1999	2001-2005	61
3	Bering Sea Tanner crab	collapse	2.1	1968-1981	1983-1985, 1988-1997	35
4	Bristol Bay red king crab (a)	collapse	2.2	1966-1980	n/a	26
5	Bristol Bay red king crab (b)	non-collapse	2.0	n/a	1986-1993, 1996-2004	20
6	Alaska Peninsula pink shrimp	collapse	2.3	1968-1979	n/a	22
7	Alaska Peninsula red king crab	collapse	2.1	1966-1983	n/a	35
8	Alaska Peninsula Tanner crab	collapse	2.0	1968-1989	n/a	30
9	Kodiak I. red king crab	collapse	2.2	1970-1982	n/a	81
10	Kodiak I. Tanner crab	collapse	2.0	1967-1986	1989-1994	62
11	Kodiak I. pink shrimp	collapse	2.1	1966-1978	1980-1986	34
12	Prince William Sound spot shrimp	collapse	1.8	1969-1988	n/a	7
13	Southeast red king crab	collapse	1.9	1969-1985	n/a	36
14	Southeast spot shrimp	non-collapse	2.2	n/a	1976-2009	80

4.1). Our unit of spatial analysis was the ADF&G statistical area, which were designed to divide larger management regions into general habitat types (inshore/offshore) and by geographic features (e.g., various bays and islands) in order to monitor the spatial distribution of fishing effort and the spatial status of stocks. The individual fisheries used in our analysis reflect independent stocks based on understanding at the time that management areas were defined, and the idea that fisheries in our study are independent is supported by observations of non-simultaneous collapse among different fisheries for the same species (Orensanz et al. 1998). Because the spatial area exploited by fleets increases as fisheries develop, areas with zero reported catch early in time series likely indicate an absence of fishing effort. Additionally, available records did not always allow us to determine if zero-catch areas had actually been open to fishing in a given season. Because we could not determine if zero-catch areas reflected the absence of effort or localized depletion of stocks, we only used statistical areas with non-zero catches in our analysis. The annual average number of active statistical areas in different fisheries ranged between 7 and 81 (Table 4.1).

Catch per unit effort (CPUE) data were available only for a subset of fisheries in this study, so we used catch data, rather than CPUE, for analysis in order to provide consistency for hypothesis tests across multiple fisheries. We defined fishery collapse as any situation where total catch declined 75% or more within three years or less, with no recovery to pre-collapse levels in the subsequent five years. Twelve fisheries met this definition of collapse, and one fishery (Southeast Alaska spot shrimp) never collapsed (Fig. 4.2A). The Bristol Bay red king crab fishery collapsed in 1981, and in the three decades since then, catches have been stable at 6-16% of peak pre-collapse levels, reflecting a successful rebuilding effort that has stabilized the stock at a fraction of its pre-collapse size (Kruse et al. 2010). We judged that this persistence and stability justified treating the post-collapse fishery as an established alternate state. We therefore treated data from 1966 (the start of the time series) to 1980 as an example of a collapsing fishery, and, after a five year transitional period, we treated the data from 1986 to 2004 (the last year before IFQs were instituted) as a second example of a non-collapsing fishery (Fig. 4.2A). Our study therefore contained 12 collapsing and two non-collapsing fisheries. While examples of non-collapsing

Fig. 4.2 (A) Catch time series included in study, plotted relative to maximum catch size for each fishery. Collapse points used in analysis are indicated by vertical dashed lines. Note that Bristol Bay red king crab data were separated into collapsing and non-collapsing periods for analysis. (B) Sample size (number of active statistical areas) by fishery and year. Horizontal dashed lines indicate mean *n* for each fishery. Missing years within time series were either years of identified collapse, which were not used in analysis, or years with zero catch for the fishery.



salmon and groundfish fisheries are available from our study region, including these populations would have resulted in conflation of taxonomic differences with population trajectories, as our study would have compared mostly crustacean, collapsing fisheries with mostly fish, non-collapsing fisheries (Anderson and Piatt 1999, Litzow 2006). Low (or no) replication at the level of populations or ecosystems is a common feature of empirical studies of regime shift indicators at spatial scales greater than laboratory microcosms, and the population-level replication in our study compares favorably with that of previous empirical studies (e.g., Litzow et al. 2008, Carpenter et al. 2011, Lindegren et al. 2012b, Seekell et al. 2012).

Analysis

The time series in our study were too short for meaningful analysis of temporal regime shift indicators (e.g., variance and autocorrelation), but large samples of spatial units for most fisheries (Fig. 4.2B) provided the opportunity for powerful tests of proposed spatial regime shift indicators. While increasing spatial correlation has been proposed as a particularly informative leading indicator of regime shifts in modeling studies (Dakos et al. 2012), the irregular spacing of statistical areas in our study precluded the calculation of this metric. We therefore restricted our analysis to changes in spatial variability and skewness.

Selection of an appropriate measure of variability is a critical consideration in studies of ecological variability (Fraterrigo and Rusak 2008). Catch data in our study were highly (positively) skewed, and the coefficient of variation, one of the more common measures of variability, produces systematic errors when used with skewed data (McArdle et al. 1990). We therefore used the standard deviation of log-transformed data (hereafter "SDL"), which is justified by Taylor's power law, which relates the mean and variance of density (N) as

$$\mathrm{var}(N) = \alpha \bar{N}^{\beta}.$$

For populations with scaling parameter $\beta = 2$, the SD and mean of log-transformed data are independent of each other (McArdle et al. 1990). We confirmed that values of $\beta = 2$ generally described mean-variance scaling for the populations in our study (mean $\beta = 2.06 \pm 0.14$ [SD], Table 4.1), suggesting that SDL was an appropriate metric for our analysis. To guard against the possibility of weak relationships

between the SD and mean of log-transformed data in situations where β was slightly different from 2, we included the mean of log-transformed data as an explanatory variable for all hypothesis tests concerning SDL values. We also guarded against any potential effect of varying sample size on SDL or skewness by including sample size (number of active statistical areas) as an explanatory variable in all analyses.

Our analysis consisted of testing three hypotheses concerning generic spatial indicators for regime shifts:

H_1: Spatial variability in catch increases prior to population collapse

H_2: Skewness in spatial catch distribution increases prior to population collapse

H_3: Increased variability is a transient phenomenon associated with collapse

We began tests of H_1 and H_2 by plotting annual-scale trends in SDL and skewness (i.e., the slope of the linear trend for the parameter of interest) for each collapsing fishery. This analysis was conducted with linear regression including the sample size and the mean of log-transformed data as explanatory variables, using estimates of residual standard errors pooled across all 12 collapsing fisheries with package "nlme" (Pinheiro and Bates 2000) in the computer language R (R Development Core Team 2010). Because the sampling unit for testing H_1 and H_2 is the individual fishery, we used global estimates of trends in the parameter of interest (i.e., the slope of the linear trend over time) across all collapsing fisheries to test our hypotheses. This analysis again used package "nlme", employing either full random-effects models (i.e., random-effect intercepts and slopes) or mixed-effects models (random-effect intercepts and fixed-effect slopes; Pinheiro and Bates 2000). Both random- and mixed-effects models estimated first-order autocorrelation in the residuals as a separate parameter, and Akaike's Information Criterion (AIC) was used to select the best model for tests of each hypothesis. We also used the best model, as determined by AIC, to test for "false positives" by comparing slopes between collapsing and non-collapsing fisheries. Trends in SDL and skewness for collapsing fisheries were calculated up to the year prior to collapse, while trends for non-collapsing fisheries were calculated across entire time series. These tests were one-tailed, since the hypotheses predict rising values of SDL and skewness (positive slopes) prior to collapse. Comparisons between collapsing and non-collapsing

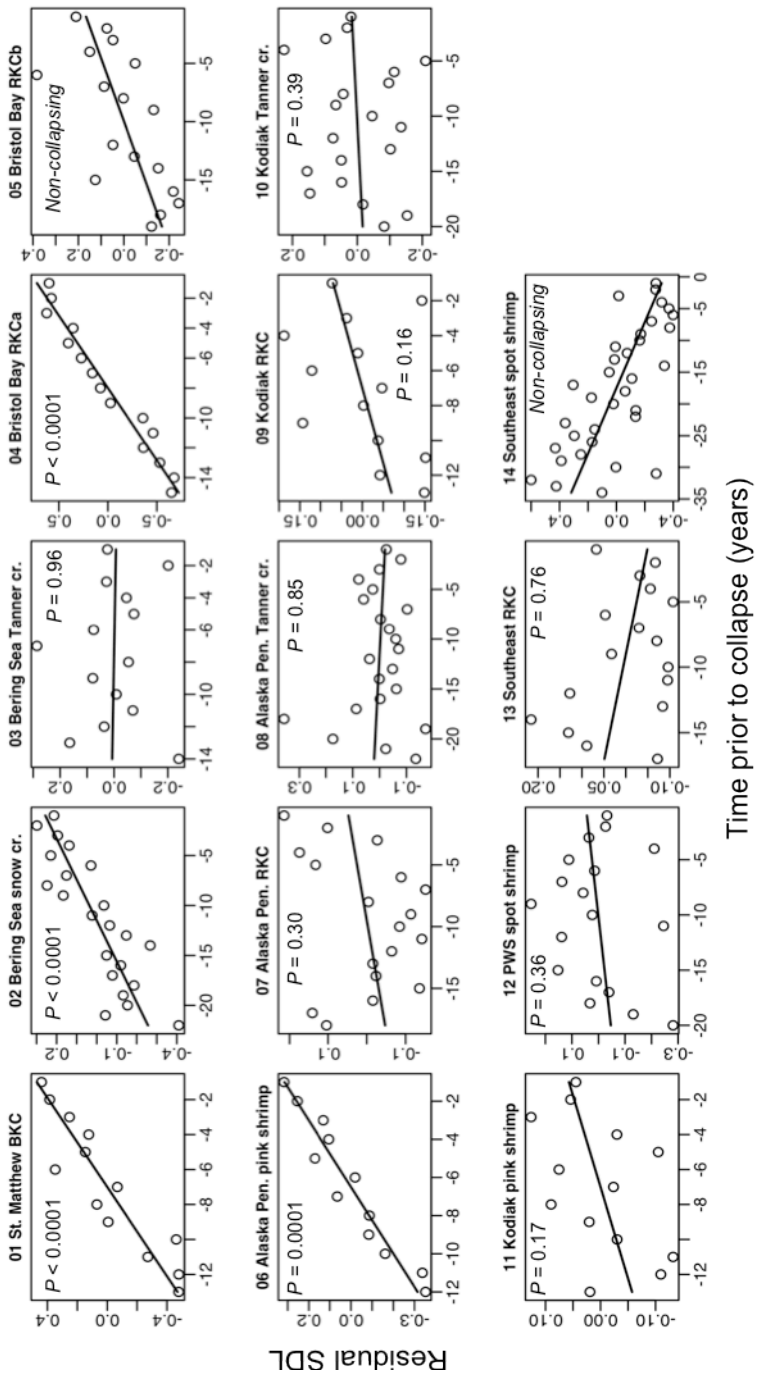


Fig. 4.3 Increasing spatial variability as a predictor of fisheries collapse: partial residual plots of SDL (SD of log-transformed data) vs. years prior to collapse. Plotted data are predicted SDL values after effects of mean of log-transformed data and sample size have been accounted for. Lines are best-fit linear trends, with associated one-tailed *P*-values testing hypothesis of increasing variability prior to collapse. Random-effects model showed strong evidence of increasing variability across all collapsing fisheries ($P = 0.0002$). Trends are indicated for non-collapsing fisheries, but *P*-values are not plotted as these fisheries were not included in hypothesis test for pre-collapse behavior.

fisheries were also one-tailed, as H_1 and H_2 predict a stronger tendency for increasing SDL and skewness (i.e., greater slopes for linear trends) for collapsing than non-collapsing fisheries. A total of eight fishery-year combinations (i.e., 5% of the 278

cumulative years of data, Fig. 4.2B) had sample sizes of 3-5, and we dropped these data from analysis for H_2, since we judged that $n = 6$ was the minimum sample size capable of producing informative skewness estimates.

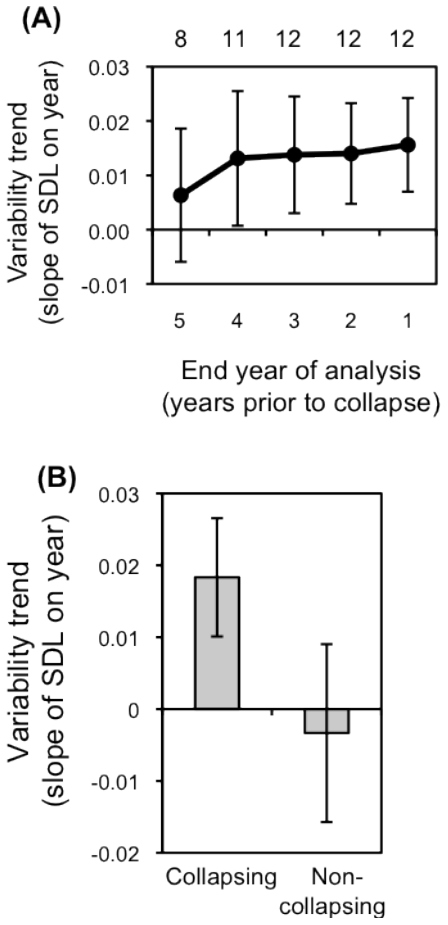


Fig. 4.4 (A) Length of potential warning from rising spatial variability: estimates of trend in SDL (slope on year) across all collapsing fisheries for analysis periods ending 1-5 years prior to collapse. Sample sizes (number of fisheries with $n \geq 10$ years of data for different analysis periods) at top of panel. Random-effects models showed significant increases in variability, across all fisheries, for data ending 1-4 years prior to collapse (one-tailed $P \leq 0.02$). (B) "False positives" test: estimates of trend in variability across all collapsing and non-collapsing fisheries (random-effects model, one-tailed $P = 0.04$). All error bars = 95% CI.

If either H_1 or H_2 were supported, we assessed at what point in time the indicator in question might generate a warning by curtailing the data included in analysis 1-5 years in advance of the collapse, and again using either fixed- or random-effects models (depending on AIC results) to estimate trends in spatial variability across fisheries. These estimates were again subjected to one-tailed tests, which evaluated our ability to detect trends in regime shift indicators from 1 to 5 years prior to a collapse.

Analysis for H_3 included fisheries for which at least 5 years of post-collapse data were available; shorter time series were judged adequate in this case because we were estimating a single parameter (mean variability) for each time series, rather than the trend in variability over time. Pre- and post-collapse SDL estimates were compared with ANCOVA. Finally, all parameter trend estimates are presented with associated 95% confidence intervals (CI).

Results

H_1: Spatial variability in catch increases prior to population collapse

This hypothesis was supported. Best linear fits for nine of the twelve collapsing fisheries showed positive slopes for SDL over time (i.e., increases in spatial variability) prior to

collapse (Fig. 4.3). While only four of the twelve individual collapsing fisheries showed statistically significant increases in variability prior to collapse (one-tailed $P \leq 0.0001$), the random-effects model, accounting for the effects of sample size and mean values of log-transformed catch, showed strong evidence for increasing variability prior to collapse across all twelve fisheries (estimated mean slope of SDL over time = 0.016 ± 0.009, $t_{182} = 3.57$, one-tailed $P = 0.0002$). In this case the random-effects model was superior to the mixed-effects model (ΔAIC = 2.54). Across all collapsing fisheries, the random-effects model showed a significant negative relationship between SDL and mean values of log-transformed data (coefficient = -0.067 ± 0.060, $t_{182} = 2.19$, two-tailed $P = 0.03$), and a significant positive relationship between SDL and sample size (coefficient = 0.002 ± 0.0017, $t_{182} = 2.82$, two-tailed $P = 0.005$), confirming the need to control for these effects. When trends were estimated across all collapsing fisheries, we found that statistically significant, increasing trends in spatial variability could be detected from 1-4 years prior to fishery collapse (one-tailed $P \leq 0.02$, Fig. 4.4a). Finally, the random-effects model showed a significantly greater slope of spatial variability on year for collapsing (slope = 0.018 ± 0.008) than non-collapsing (slope = -0.003 ± 0.012) fisheries ($t_{230} = 1.81$, one-tailed $P = 0.04$, Fig. 4.4b).

H_2: Spatial skewness in catch increases prior to population collapse

Our data clearly did not support this hypothesis: best linear fits for only four of the 12 collapsing fisheries showed positive trends in skewness prior to collapse, and only one of these was statistically significant (Alaska Peninsula Tanner crab, one-tailed $P = 0.03$, Fig. 4.5). The mixed-effects model was superior to the random-effects model for estimating the trend in pre-collapse skewness across all collapsing fisheries (ΔAIC = 2.26); however, this model failed to reject the null hypothesis (estimated slope of skewness on year = -1.05 ± 2.20, $t_{172} = 0.94$, one-tailed $P = 0.83$). Results of this hypothesis test were not different when the skewness of log-transformed data was analyzed (estimated slope of skewness on year = 0.59 ± 2.01, $t_{172} = 0.58$, one-tailed $P = 0.28$).

H_3: Increased variability is a transient phenomenon associated with collapse

This hypothesis was also not supported by our data. We found significantly higher spatial variability in catches in post-collapse (mean n = 15 years) versus pre-collapse (mean n = 17 years) fisheries (ANCOVA with fishery identity, sample size, mean of log-transformed catches and pre-or post-collapse state as explanatory variables, model $F_{7,126} = 10.33$, $P < 0.0001$; effect of pre- vs. post-collapse state, $P < 0.0001$; Fig. 4.6).

Discussion

Fishing effects in marine ecosystems may act synergistically with other forcing mechanisms, notably climate change, coastal eutrophication and habitat loss (Harley et al. 2006, Crowder et al. 2008), in a way that makes regime shifts and "ecological surprises" likely (deYoung et al. 2008). Given the poor global record of achieving fisheries sustainability (Worm et al. 2009), a tool that would provide early warning of impending non-linear behavior in exploited stocks and communities would be an important addition to fisheries management. Our results support the use of one proposed generic regime shift indicator – increased spatial variability – to predict fisheries collapse. While the considerable noise inherent in many marine populations creates a challenge for detecting statistically significant trends (Nicholson and Jennings 2004), and the time series in our study were quite short (mean = 17 years prior to collapse), we found evidence for increasing variability prior to collapse when an overall trend in variability was estimated across all collapsing fisheries (P = 0.0002). However, although sample size for most fisheries (Fig. 4.2B) achieved the sampling intensity (n = 28 – 50) found necessary to detect spatial indicators of regime shifts in experimental manipulations (Carpenter et al. 2011, Seekell et al. 2012), we only detected statistically significant increases in spatial variability prior to collapse in four of 12 collapsing fisheries (Fig. 4.3). The considerable difference among populations in variability trends that we observed suggests that efforts to use this indicator for single populations may require levels of statistical power that are rarely available in management situations (Perretti and Munch 2012). Tests for change in variability across multiple populations, as we have presented here, may be a more realistic approach.

While the statistical power of our test for "false positives" was severely limited by the small sample of non-collapsing fisheries (n = 2), we were able to reject

the null hypothesis of no difference in trends of spatial variability between collapsing and non-collapsing fisheries (one-tailed $P = 0.04$, Fig. 4.4b). Thus, if managers of historical Alaskan crustacean fisheries had been monitoring trends in the spatial

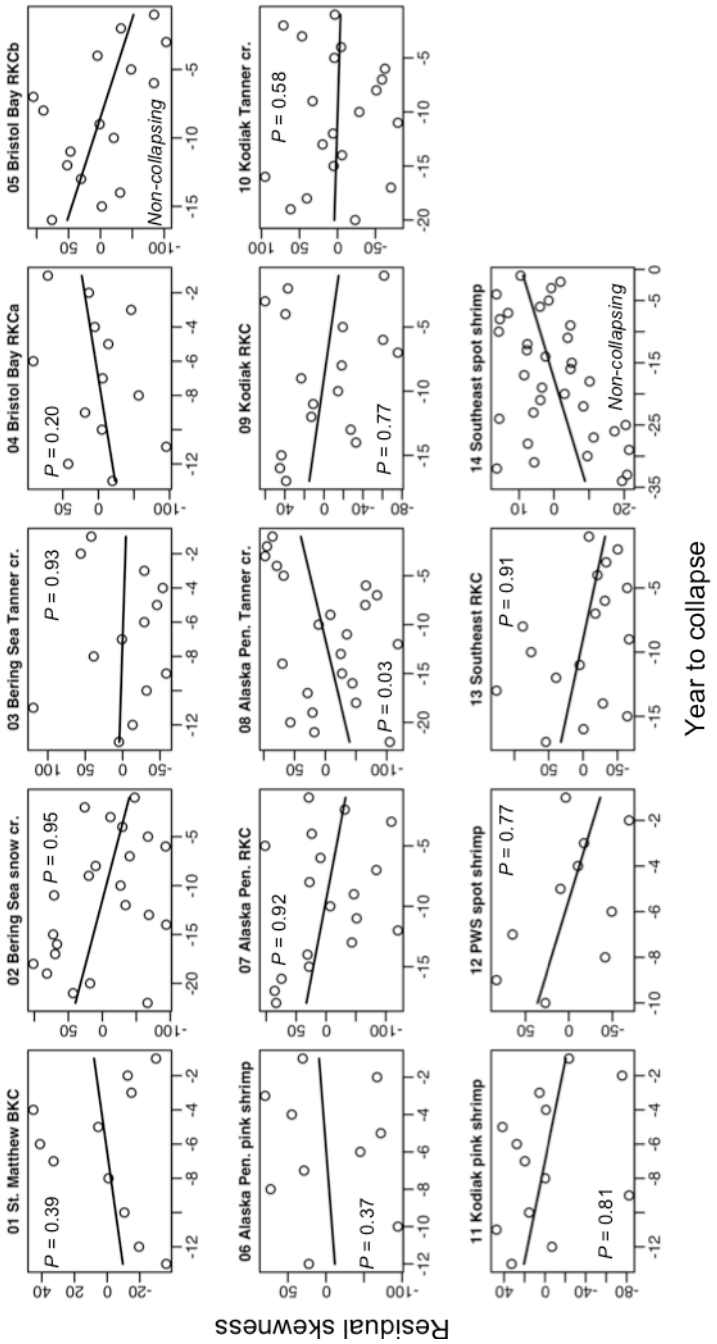


Fig. 4.5 Trends in spatial skewness of catch across all fisheries: partial residual plots after effects of sample size have been accounted for. Lines illustrate best-fit linear trends, with associated one-tailed *P*-values testing hypothesis of increasing skewness prior to collapse. Trends are indicated for non-collapsing fisheries, but *P*-values are not plotted as these fisheries were not included in hypothesis test for pre-collapse behavior. Random-effects model showed no evidence of pre-collapse increases in skewness across all collapsing fisheries (one-tailed $P = 0.83$).

variability of catches, they would have had early warning of impending collapse, and would also have had a basis for distinguishing fisheries in danger of collapse from those that were not.

Critically, analysis across multiple fisheries was able to detect statistically significant increases in variability up to 4 years prior to collapse (Fig. 4.4a). The question of whether adequate early warning is generated for an effective management response is central to evaluations of regime shift indicators (Biggs et al. 2009, Contamin and Ellison 2009). The immediate mechanism leading to fisheries collapses may be spikes in fishing mortality 1-3 years before the collapse is reached (Myers et al. 1996), which suggests that a 4-year warning might be adequate for decisive management action to stave off collapse. However, we grouped different fisheries relative to the number of years prior to collapse, which is only possible in a retrospective analysis. Since individual fisheries actually collapsed in different years

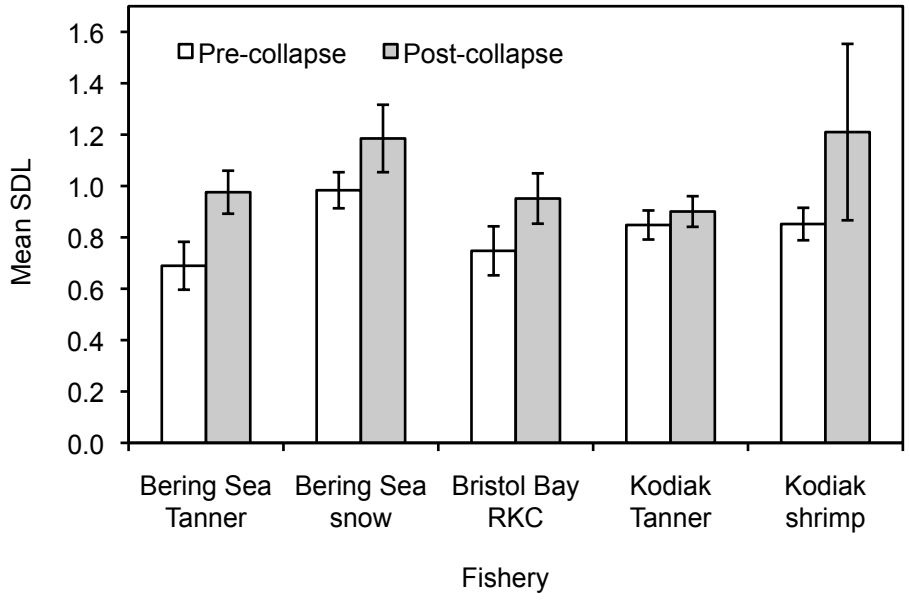


Fig. 4.6 Evidence of persistent increases in spatial variability in post-collapse fisheries, relative to pre-collapse state (ANCOVA, pre- vs. post-collapse state, $P < 0.0001$). Error bars = 95% CI.

(Fig. 4.2A), the statistical power that we gained by synchronizing fisheries relative to collapse year would not be available to managers conducting a monitoring study. This observation highlights the need to develop adequate statistical power by applying regime shift indicators to as many populations as possible when used in a fisheries context, ideally for a diverse set of species, since community reorganizations associated with fishery collapses often affect taxonomically diverse populations at

multiple trophic levels (Hare and Mantua 2000, Choi et al. 2004). Furthermore, the 1976/77 PDO shift also set into motion changes in internal community dynamics, such as the direction of trophic control (Litzow and Ciannelli 2007), that might have doomed crustacean stocks to collapse regardless of changes in exploitation rate. This is a potential problem for any early warning of a possible regime shift in complex systems, such as the Bering Sea and Gulf of Alaska continental shelf ecosystems, where the dynamics underlying non-linear behavior are not understood. In such instances, there is little ability to provide scientific advice for an appropriate management response if declining resilience is detected by regime shift indicators. However, fisheries are typically the leading perturbation to marine ecosystems (Jackson et al. 2001), and catch rates are much more amenable to rapid management adjustment than other sources of perturbation, like habitat loss or climate change (Biggs et al. 2009). We therefore suggest that catch reductions are an appropriate response in any situation where evidence of an impending shift in exploited stocks is observed. Indeed, the ability to provide an early warning in systems where the underlying dynamics are not understood is one of the great potential benefits of generic indicators (Carpenter and Brock 2006, Guttal and Jayaprakash 2009). This contrasts with other possible spatial indicators of impending regime shifts (e.g., scale-invariant distributions of patch size), which require detailed knowledge of underlying system dynamics to be applied appropriately (Scheffer et al. 2009).

For regime shift indicators to be used by managers, reference points are needed to allow the risk of a regime shift to be inferred from the observed magnitude of change in the indicator. While a properly designed laboratory experiment can produce such reference points in terms of units of variance increase in indicators (Drake and Griffen 2010), a single observational study cannot. Aside from the question of whether the rates of increase in variability that we observed can be generalized to other fisheries or other ecosystem types, the fact that collapsing fisheries (n = 12) greatly outnumbered non-collapsing fisheries (n = 2) in our study means that our observations are greatly skewed towards the pre-collapse state, and we lack a range of observations in non-collapsing fisheries to define the full range of variability that might be observed at different levels of risk for a regime shift. Given the data available to us, the only recommendation we can make to managers is that statistically significant increases in the spatial variability of catches across multiple populations may indicate an elevated risk of collapse within 1-4 years, and may

warrant precautionary reductions in harvest levels until trends in variability are stabilized. We also note a corollary: if increasing spatial variability is a characteristic of stocks that are approaching collapse (Fig. 4.3), and if this variability is driven by fishing (see below), then preventing increases in variability (e.g., through spatially explicit harvest rules) suggests a management strategy for preventing collapse.

We found no support for the use of rising skewness in catch data as a leading indicator of fisheries collapses. There was no evidence of a linear increase in skewness prior to collapse, nor did time series show peaks in skewness around collapse points (Fig. 4.5). The average sample size for collapsing fisheries (n = 37, Table 4.1) was large enough to rule out inadequate statistical power as the cause for failing to reject the null hypothesis (Guttal and Jayaprakash 2008). Though they have a strong theoretical basis (i.e., asymmetry in the landscape picture of ecosystem dynamics near a bifurcation; Guttal and Jayaprakash 2008, Scheffer et al. 2009), increases in spatial skewness near a regime shift have to our knowledge not been demonstrated empirically. Fisheries catch data are typically highly skewed, so it may be that expectations derived from observing landscape asymmetry in minimal ecosystem models that do not assume high ambient skewness may not be applicable in fisheries systems. Another issue in empirical tests of model-generated regime shift indicators is the presence of noise in real ecological data (e.g., due to observational error) that is not captured by the stochastic dynamics of the model (Guttal and Jayaprakash 2008, Contamin and Ellison 2009). This issue is particularly important when fisheries catch data are being used, as in this study. Because catchability is non-constant and usually unknown, the relationship between catch and abundance typically cannot be estimated (Maunder et al. 2006, Branch et al. 2011). This situation creates a recognized, but unquantifiable, source of noise between the parameter proposed for increasing variability (abundance) and the parameter tracked by managers (catch). While inferring population collapse from catch or CPUE data is often problematic (Maunder et al. 2006, Branch et al. 2011), depressed crustacean fisheries catches in Alaska are well known to reflect persistently low levels of abundance in the underlying populations. Evidence demonstrating collapses in the populations in our study includes both abundance estimates from decadal-scale fisheries-independent surveys in the Gulf of Alaska and Bering Sea (Anderson and Piatt 1999, Loher and Armstrong 2005, Litzow 2006, Litzow and Ciannelli 2007) and model-derived estimates of demographic parameters (Zheng and Kruse 2000, Zheng

et al. 2001, Zheng and Kruse 2006, Bechtol and Kruse 2009). Decadal-scale periods of reduced population size for Alaskan crustaceans are also believed to reflect large-scale ecological responses to the 1976/77 PDO regime shift (Anderson and Piatt 1999, Hare and Mantua 2000, Litzow 2006, Litzow and Ciannelli 2007). Using management data, such as the catch data in this study, inevitably involves accepting limitations that are not present in data from a properly designed experiment. However, given the fisheries-independent support outlined above, we believe that it is reasonable to assume that collapsing commercial catches in this instance reflect persistent change in underlying populations.

As exploited stocks are driven to collapse, the population distribution contracts to high-quality habitat areas, such that the proportion of high population density areas remains fairly constant, while the proportion of low- and medium-density areas falls (Hutchings 1996). This dynamic suggests a mechanism by which commercial fishing might drive the expected increase in spatial variability as collapse approaches; increases in temporal variability in exploited stocks due to fishing-induced truncation in age structures (Hsieh et al. 2006, Anderson et al. 2008) have previously been invoked as a mechanism that may induce non-linear behavior in marine ecosystems (Scheffer et al. 2009). Fishing-driven retractions in distribution, and resulting loss of heterogeneity of habitat, may also act synergistically to increase sensitivity of exploited stocks to climate variability (Hsieh et al. 2008b). We presume that the increase in spatial variability in catch data prior to collapse (Fig. 4.3) is driven by underlying increases in the variability of abundance. Standardized fisheries-independent surveys of crustacean stocks in Alaska generally began in the early 1980s, so pre-collapse measurements of abundance are available for few stocks. However, one available standardized survey from a single bay in the Gulf of Alaska does show rising variability in the abundance of Pandalid shrimp immediately around a late-1970s community reorganization (Litzow et al. 2008), providing limited confirmation that the increased variability in catch that we observed reflected patterns of underlying abundance.

Expectations of rising variability prior to regime shifts stem from model observations of critical slowing down in system response to perturbation as a bifurcation is approached (Scheffer et al. 2009). Since critical slowing down is observed only around the bifurcation, models predict a transient increase in variability around the regime shift (Carpenter and Brock 2006, Biggs et al. 2009, Guttal and

Jayaprakash 2009). This was not the case in our study. At the temporal scale of our analysis (mean n = 17 years pre-collapse, 15 years post-collapse), variability was significantly greater in the post-collapse than pre-collapse state (Fig. 4.6). Rapid (annual-scale) change in community structure is a central feature of PDO-forced regime shifts in North Pacific ecosystems (Hare and Mantua 2000), and peak response to climate variability by continental shelf communities in Alaska is observed at lags of 2-4 years (Litzow 2006), suggesting that our observation of increased variability extended past the period of ecological transition. We interpret this persistent increase in variability as being more consistent with fishing effects on variability, rather than critical slowing down. For fisheries managers, this distinction is perhaps not very important – as long as rising spatial variability is a signal of an increasing risk of stock collapse (Fig. 4.3), the exact mechanisms behind the relationship are not critical. However, the suggestion that mechanisms other than multiple stable state dynamics may have produced the elevated variability that we observed, coupled with the failure of rising skewness as an early indicator of collapse, suggest that caution is warranted when generalizing our results to other ecosystem types.

While multiple stable state dynamics have been formally demonstrated in marine ecosystems (e.g., Hsieh et al. 2005, Schröder et al. 2005, Hsieh and Ohman 2006), they are often simply inferred from abrupt shifts in ecological time series (Scheffer et al. 2001). However, other types of time series variability may cause these sudden shifts (Rudnick and Davis 2003). At times ecologists have uncritically embraced multiple stable states as a conceptual model for understanding abrupt community shifts even though available evidence supports a more parsimonious explanation (Dudgeon et al. 2010). Regime shift indicators suggest a solution to one of the leading problems in applied ecology, are presented as being ubiquitous in a wide range of complex systems, and are generating much interest in high-profile journals (e.g., Biggs et al. 2009, Scheffer et al. 2009, Drake and Griffen 2010, Carpenter et al. 2011). However, our failure to detect pre-collapse increases in skewness, and, to a lesser extent, our observation of persistent post-collapse increases in variability, suggest that these indicators need to be applied cautiously in systems where non-linear dynamics are either not formerly defined or not understood. Empirical tests are important in this context. Given the possibility of a "band wagon" effect for such a novel and promising approach to detecting regime shifts, we suggest

that studies producing negative results may be particularly useful in defining the actual utility of these indicators.

Acknowledgments

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Chapter 5 Detecting complex ecological change in data-limited situations: an example from southeast Australia

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Abstract

The ability to detect abrupt ecological "regime shifts" in a data-limited setting was investigated, using southeast Australian ecosystems as a model. Specific goals were: 1) testing for coherent patterns of community-level biological variability in the region; 2) evaluating the evidence for either gradual change or abrupt shifts in regional climatic and biological variability; and 3) evaluating the ability of leading modes of regional and basin-scale climate variability to explain community-level biological variability. Community variability was summarized for 1968-2008 with the first two principal components ($PC1_{biol}$, $PC2_{biol}$) of recruitment estimates for six fish stocks and reproductive parameters for four seabird species; regional climate was summarized for 1953-2008 with the first two PCs ($PC1_{reg}$, $PC2_{reg}$) for three parameters (sea surface temperature, sea surface salinity, surface nitrate) measured at two stations; and basin-scale climate variability was summarized for 1950-2012 with the mean South Pacific SST (SST_{mean}) and the first two PCs ($PC1_{sst}$, $PC2_{sst}$) of detrended South Pacific SST. PC1-2_{biol} explained 45% of total community variability, demonstrating coherent community-level variability comparable to Northern Hemisphere systems. PC1-2_{SST} showed low-frequency variability similar to "regime" behavior observed in other ocean basins, and $PC1_{SST}$ was correlated with both the Multivariate ENSO Index and the Pacific Decadal Oscillation Index. $PC1_{SST}$ also explained 14.9% of variability in $PC1_{reg}$, confirming a role of basin-scale, low-frequency climate variability as a driver of regional ecosystem dynamics. However, the best trend models for PC1-2_{reg} and $PC1_{biol}$ all invoked linear or nearly-linear trends, consistent with a dominant secular trend in the climate and biology of southeast Australian shelf ecosystems. However, analysis of a large set of previously-published biological time series from the North Pacific (n = 64) suggests that studies using fewer than ~25 biological time series, such as this one, may be unable to detect regime shifts. The development of long-term biological observations is needed for understanding change in many marine ecosystems globally.

Keywords: Australia; climate change; climate variability; data needs; ecosystem disturbance; fisheries; recruitment; regime shift; seabirds

Introduction

Abrupt ecological "regime shifts" provide less opportunity for adaptation than do more gradual ecological changes (Hamilton et al. 2003, Hamilton et al. 2004), so recognizing the potential for regime shifts is an important step towards understanding the impacts of external perturbations on marine ecosystems. Documenting regime shifts has typically required decades of biological observations over large spatial scales (Möllmann and Diekmann 2012), however, such long-term observations are rare in many marine ecosystems (Richardson and Poloczanska 2008, Brown et al. 2011). An important unanswered question is whether complex patterns of change, including abrupt shifts that are coherent across a community, can be detected in the data-limited situation that is typical of many marine systems.

Southeast Australia continental shelf systems are one such region where continuous multi-decadal biological observations are extremely scarce (Poloczanska et al. 2007, Frusher et al. 2014). Most studies of ecological change in the region have relied on comparisons with historical data or anecdotal information, often with decades of missing values separating periods of observation (e.g., Johnson et al. 2011, Last et al. 2011). The region is frequently referred to as a "global warming hotspot" – observations since 1944 at Maria Island (42° 36'S, 148° 14'E) show rapid surface warming (~0.23 °C / decade, or roughly 3.7 times the global rate) associated both with the southward extension of the East Australia current (EAC; Ridgway 2007), and with basin-scale change in the southwest Pacific (Bindoff and Church 1992, Holbrook and Bindoff 1997). Regional trends in surface temperature and salinity have a strong linear/secular component and have been associated with a variety of ecological responses (Johnson et al. 2011, Frusher et al. 2014).

In addition to this secular trend, there is reason to believe that low frequency climate variability might also play an important role in southeast Australian marine ecosystems. Extension of the EAC shows a strong decadal pattern over the linear trend (Ridgway 2007), and the signatures of various large-scale climate modes with red-shifted temporal variability appear in time series of several regional climate parameters. For example, leading modes of interdecadal Pacific climate variability are known to affect hydrology in southeast Australian terrestrial ecosystems (McGowan et al. 2010), rainfall in the western Pacific (Hsu and Chen 2011), and sea level pressure anomalies, cyclone/anticyclone behavior and sea surface temperature

(SST) in the southwest Pacific (Pezza et al. 2007, DeLong et al. 2012). These observations of low-frequency climate variability suggest the possibility of red noise internal climate variability as a mechanism forcing sudden ecological change, as has been described in the Northern Hemisphere (Rudnick and Davis 2003, Overland et al. 2006, Di Lorenzo and Ohman 2013). Furthermore, some suggestions of abrupt change in life history parameters of individual species in the region have been made (Ziegler et al. 2007, Wayte 2013), which are consistent with observations of abrupt shifts in life history parameters of populations involved in Northern Hemisphere shifts (e.g., Wilderbuer et al. 2002). However, due to the scarcity of long-term biological observations, the degree to which population-level variability is coherent across southeast Australian communities, and whether coherent community variability is expressed in abrupt shifts of the sort that have been indentified in many Northern Hemisphere systems (Möllmann and Diekmann 2012), remains unknown. Recognizing whether regime shifts occur in the region is important for gauging the likelihood of future ecological surprises (sensu Doak et al. 2008), in addition to guiding efforts to adapt to climate change, particularly as this region supports the largest commercial fisheries in Australia (Koehn et al. 2011).

The objective of this study is to examine available long-term climatic and biological observations for evidence of abrupt shifts in southeast Australian marine ecosystems. Specific goals are to: 1) test for coherent patterns of community-level biological variability in the region; 2) compare statistical models of secular change and abrupt shifts for describing regional climatic and biological variability; and 3) evaluate the ability of leading modes of regional and basin-scale climate variability to explain community-level biological variability. An additional goal is to evaluate the ability to detect complex temporal patterns of biological variability (i.e., abrupt shifts) in a data-limited situation.

Materials and Methods

Terminology

Low-frequency climatic and biological variability have often been investigated in the context of abrupt switches between persistent states, or "regime shifts". While the regime shift concept has been important in introducing the ideas of thresholds, non-

linearities and non-stationary driver-response relationships in marine ecology, the utility of the concept is ultimately limited by a lack of an agreed-upon definition. In particular, marine ecologists have often used *ad hoc*, system-specific definitions for what constitutes a regime shift (Lees et al. 2006), and the term enjoys a different currency in marine and general ecology (Litzow and Mueter 2014). Additionally, climate regime shifts have often been invoked in a search for periodicity in large-scale climate modes (Minobe 1999, Zwolinski and Demer 2012, Hatch 2013), but consensus has grown among physical oceanographers that sudden climate shifts are more parsimoniously explained by red noise variability (Rudnick and Davis 2003, Hsieh et al. 2005, Overland et al. 2006, Di Lorenzo and Ohman 2013). Because red noise behavior explicitly rules out any periodicity or predictability, this consensus has cast much of the regime shift literature as slightly outmoded (Doney and Sailey 2013). Accordingly, low-frequency variability in leading climate modes is hereafter referred to as "interdecadal variability". This term is meant to encompass complex trends and sudden shifts, described statistically with >> 1 model degrees of freedom (df), as opposed to more linear (secular) trends, described by ~ 1 model df.

Data

The central problem in studies of low-frequency variability in southeast Australian ecosystems is the paucity of available long-term time series of biological parameters (Frusher et al. 2014). We identified suitable time series by searching the peer-reviewed literature, agency reports and other gray literature, and through direct contact with data holders. When evaluating biological data for use in this study, the criteria for inclusion were: 1) suitable length (≥ 25 years of observation); 2) measurement of parameters expected under life history theory to show sensitivity to high frequency (i.e., annual) environmental variability (e.g., recruitment or breeding biology parameters) rather than parameters that are expected to be buffered against annual-scale environmental variability (e.g., commercial catch or adult survival for long-lived species; Cairns 1988, Pankhurst and Munday 2011); and 3) in the case of model-derived parameter estimates, adequate support with empirical data. Biological time series that met these criteria mostly began in the late 1960s and early 1970s and came from two sources: long term observations of seabird breeding biology at Phillip

Island., Victoria (38° 29' S, 145° 13' E) and Montague Island., New South Wales (36° 15' S, 150° 14' E), and recruitment estimates, generated by age-structured assessment

Table 5.1 Climate and biology time series used in analysis. *m = months, y = years

Abbreviation	Name	Scientific name	Source	Time span	*n**
SST_{mean}	Mean S. Pacific SST	n/a	HadISST	1950-2012	756 m
PH nitrate	Port Hacking nitrate	n/a	IMOS	1953-2010	507 m
PH SSS	Port Hacking surface salinity	n/a	IMOS	1953-2010	595 m
PH SST	Port Hacking surface temp.	n/a	IMOS	1953-2010	590 m
MI nitrate	Maria I. nitrate	n/a	IMOS	1953-2008	477 m
MI SSS	Maria I. surface salinity	n/a	IMOS	1953-2008	528 m
MI SST	Maria I. surface temperature	n/a	IMOS	1953-2008	517 m
WT chick	Montague I. wedge-tailed shearwater chick count	*Ardenna pacifica*	David Priddell	1967-2010	44 y
Sooty chick	Montague I. sooty shearwater chick count	*A. grisea*	David Priddell	1967-2010	44 y
ST chick	Montague I. short-tailed shearwater chick count	*A. tenuirostris*	David Priddell	1967-2010	44 y
LP MLD	Phillip I. little penguin mean laying date	*Eudyptula minor*	Peter Dann	1968-2010	43 y
LP chick	Phillip I. little penguin chicks produced per pair	*E. minor*	Peter Dann	1968-2010	43 y
LP mass	Phillip I. little penguin chick mass at fledging	*E. minor*	Peter Dann	1968-2010	43 y
Morwong	Jackass morwong east recruitment	*Nemadactylus macropterus*	AFMA/CSIRO	1967-2006	40 y
Whiting	School whiting recruitment	*Sillago flindersi*	AFMA/CSIRO	1981-2006	26 y
Gemfish	Eastern gemfish recruitment	*Rexea solandri*	AFMA/CSIRO	1968-2007	40 y
Warehou	Silver warehou recruitment	*Seriolella punctata*	AFMA/CSIRO	1980-2007	28 y
Pink ling	Pink ling east recruitment	*Genypterus blacodes*	AFMA/CSIRO	1973-2009	37 y
Grenadier	Blue grenadier recruitment	*Macruronus novaezelandiae*	AFMA/CSIRO	1972-2008	37 y

models, for fish stocks managed by the Australian Fisheries Management Authority as part of the Southern and Eastern Scalefish and Shark Fishery (SESSF). The seabird data included annual chick counts for three species (wedge-tailed shearwater, sooty shearwater, short-tailed shearwater) nesting at Montague I., and three parameters (mean laying date, mean chick weight, breeding success/chicks produced per pair) for little penguins nesting at Phillip I. Of the 15 stock assessments available

for the SESSF, six produced time series of recruitment estimates that met the criteria for inclusion (eastern jackass morwong, school whiting, eastern gemfish, silver warehou, eastern pink ling and blue grenadier). Following the approach of similar studies in the Northern Hemisphere (e.g., Hare and Mantua 2000), we used recruitment estimates in analysis, rather than stock-recruit residuals. This approach incurs the cost of uncontrolled effects of stock size on recruitment, but conveys the benefit of avoiding variability associated with poorly-resolved stock-recruit relationships and uncertain stock size estimates. Sources and scientific names for all time series are presented in Table 5.1.

While biological observation began in the 1960s, regional climate data are available from the Maria Island National Reference Station beginning in 1944, and for the Port Hacking station in 1953. Data coverage for SST observations in the South Pacific is adequate to provide spatially and temporally resolved basin-scale interpolated data beginning around 1950 (Rayner et al. 2003). Accordingly, we used regional climate observations for the period 1953-2008 (the last year of data made publicly available) and basin-scale observations for the period 1950-2012; the use of climate data beginning nearly two decades before the onset of biological observations allowed more recent climate changes to be put into context, and also provided more statistical power to detect interdecadal variability in time series, and for detecting covariation between regional and basin-scale climate. Basin-scale climate variability was measured with SST data for the South Pacific (20º-56ºS, 142ºE-70ºW) accessed from the HadISST 1º x 1º gridded interpolated data set for 1950-2012 (www.metoffice.gov.uk/hadobs/hadisst/). Regional-scale climate variability was measured with SST, surface salinity (SSS) and surface nitrate from the Maria Island and Port Hacking National Reference Stations (imos.org.au). All climate data were obtained as monthly values.

Analysis

The goals of analysis were to: 1) identify leading modes of variability in data sets using principal components analysis (PCA); 2) compare hypotheses of secular change and interdecadal variability for explaining temporal variability in leading climate and biology modes; and 3) evaluate the ability of regional and basin-scale climate

variability to explain biological change. A schematic overview of the steps used in analysis is presented in Fig. 5.1.

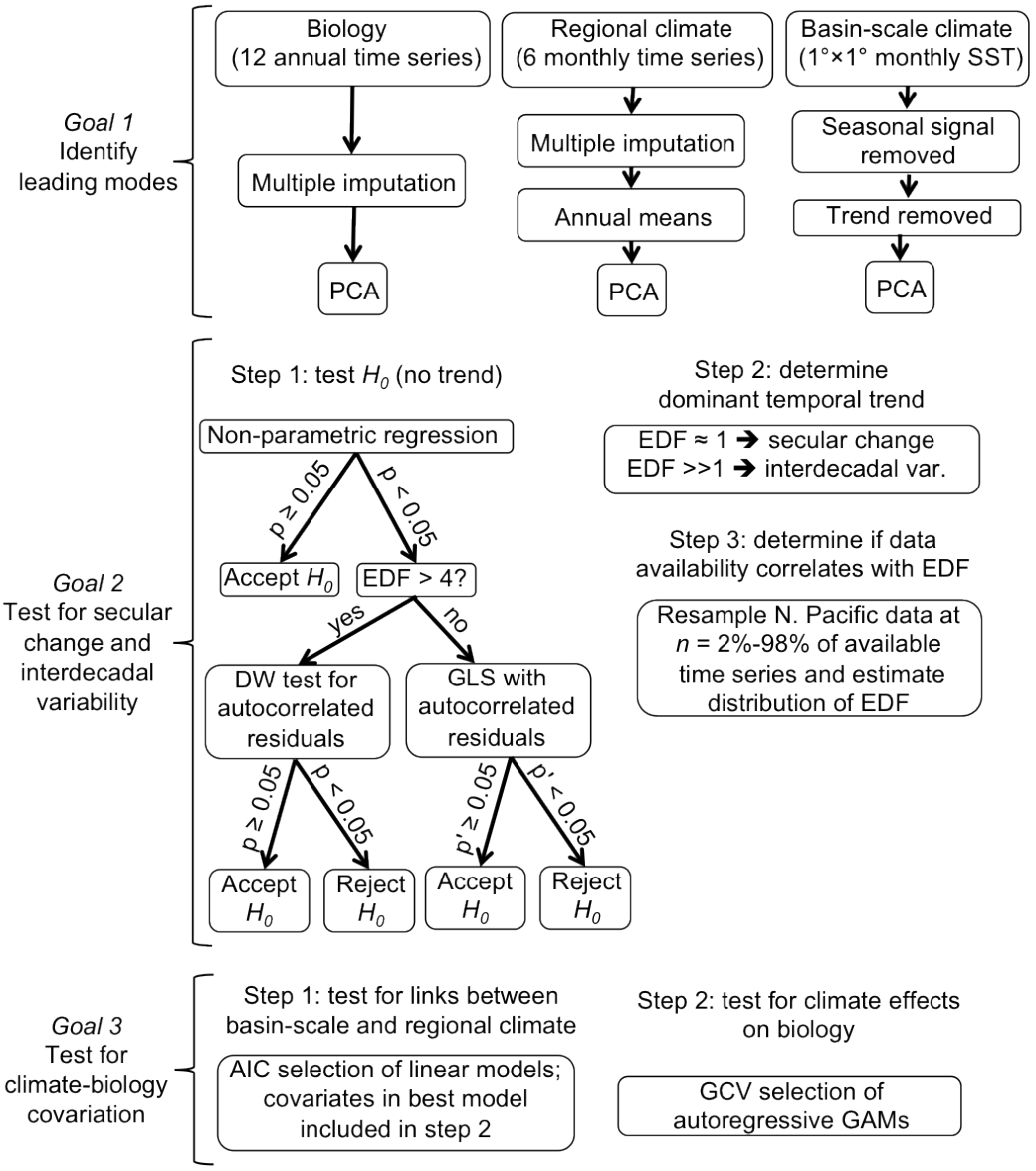

Fig. 5.1 Schematic depicting steps used in analysis.

Regional biology and climate

Available biological time series ran from 1967 to 2010; during this time 59 annual observations (11.1%) were missing. Regional climate time series ran from 1953 to 2008; during this time 858 monthly observations (21.3%) were missing. Because missing values were non-randomly distributed (i.e., clustered at the beginning and ending of time series), PC scores calculated from the incomplete data set would likely be biased. In order to obtain unbiased PC scores and to estimate the uncertainty associated with estimating missing values, a multiple imputation approach was used to fill in missing values prior to computing PC scores for each imputed dataset (Schafer 1997, Litzow et al. 2014). For the biological data set, recruitment estimates were first log-transformed to achieve normality, and eigenvectors (loadings) and eigenvalues were then calculated from a correlation matrix of the incomplete time series, using a singular value decomposition with function "svd" in the computer language R (R Development Core Team 2010). The mean and distribution of each missing value were then estimated using 100 randomly drawn imputations of the missing data that were implemented with Bayesian linear regression techniques in the R package "mice" (Van Buuren and Oudshoorn 1999). Finally, annual PC scores were estimated for each imputed dataset by applying the PCA loadings to the complete time series, and then computing the mean and standard deviation (SD) for the annual PC scores across all 100 imputed values. The SD of the annual scores allowed the uncertainty associated with estimating missing values to be quantified; if the SD for any year was greater than the mean absolute value for the corresponding PC score across all years of the time series, it was judged that too much uncertainty had been introduced by estimating missing values for further analysis to be meaningful.

In order to derive annual estimates of regional climate parameters from the incomplete set of monthly observations, missing monthly values were first estimated as the mean of 100 sets of imputed data derived with the "mice" package. Annual means of the six regional climate parameters were calculated from this imputed data set, and PCA was conducted on these annual means.

Basin-scale climate

The seasonal signal was removed from each of the 1º x 1º cells prior to any analysis of the HadISST data set. To describe leading modes of variability independent of the secular trend, time series of monthly anomalies from each cell were detrended (linear trend removed), and PCA was performed on the resulting detrended data set. This detrending approach is widely used to identify leading modes of internal climate variability independent of the secular trend (Mantua et al. 1997, Di Lorenzo et al. 2008). In order to evaluate correspondence between the modes returned by this analysis and previously-documented modes of climate variability, loading maps for the leading modes were compared with similar maps for the leading modes of global SST variability (Messié and Chavez 2011), and correlations were calculated with time series of the Multivariate ENSO Index (MEI, www.esrl.noaa.gov/psd/enso/mei/), the Pacific Decadal Oscillation Index (PDO; jisao.washington.edu/pdo/) and the North Pacific Gyre Oscillation Index (NPGO; www.o3d.org/npgo). Finally, all PCA results were evaluated with the bootstrapped-λ approach of Peres-Neto et al. (2005) to confirm that leading axes were in fact interpretable.

Secular trends and interdecadal variability

A null hypothesis of no trend in various PC time series was evaluated using non-parametric regression (penalized regression splines) implemented in R package "mgcv" (Wood 2006). The appropriate estimated degrees of freedom (EDF) for the temporal trend was selected through minimizing the generalized cross validation (GCV) score (Wood 2006); an EDF ≈ 1 indicates a near-linear trend, consistent with secular change, while an EDF $>>1$ indicates a non-linear trend, consistent with interdecadal variability. In order to account for the effect of autocorrelation in time series data, p-values for these hypothesis tests were calculated using general least squares (GLS) models with autocorrelated residuals in R package "nlme" (Pinheiro and Bates 2000). The order of the GLS model was set with the EDF selected by non-parametric regression, and the resulting probability is reported with the notation p'. However, for very complex trends (EDF > 4), interpretation of the results was complicated by the absence of a model p-value in GLS results (the restricted log-likelihood methods used to fit the GLS model estimate only parameter-specific probabilities). In these cases residuals from non-parametric regression were evaluated

for significant autocorrelation with the Durbin-Watson test in R package "lmtest"; if no significant autocorrelation was found, the p-value for the non-parametric regression was accepted.

Studies documenting large-scale interdecadal ecological variability in other ocean basins have typically had access to a larger number of long-term biological observations than are available in southeast Australia (e.g., 64 biology time series from the North Pacific in Hare and Mantua (2000) vs. 12 time series in the present study). There is some possibility that the paucity of biological observations in the study region may make it more difficult to detect complex interdecadal trends. To evaluate the role that the number of available observations plays in the ability to detect higher-order variability, the Hare and Mantua (2000) data set, as updated by Litzow et al. (2014), was used as a test case. A complete set of observations for the 64 time series was estimated using multiple imputation. A randomized resampling approach was then used to evaluate the relationship between sample size and the ability to detect complex trends, following these steps:

1. The time series were resampled at 63 different levels of completeness (i.e., with n = 1 to 63 time series included in the resample). Each level of resampling was achieved through 1,000 random selections, with replacement, of the desired number of time series.
2. The first PC was calculated for each of the 1,000 permutations at each of the 63 levels of resampling intensity.
3. A penalized regression spline model with unrestricted EDF was fitted to the PC1 time series for each permutation.
4. The median, 5^{th} and 95^{th} percentile were calculated for the 1,000 randomized EDFs for each of the 63 levels of resampling intensity and compared with the true EDF from the complete data set.

In order to test for secular trends in basin-scale climate, the mean monthly basin-wide SST anomaly was calculated from the HadISST data set. A plot of spatial change in annual SST values during 1950-2012 cell was used to evaluate the rate of SST change in southeast Australia. This plot used SST values predicted from the best-fit non-parametric regression of SST on year for each 1° × 1° cell.

Climate-biology covariation

The goal of climate-biology covariation analysis was to evaluate the ability of both basin-scale climate variability (the secular trend in mean SST and leading axes of variability in detrended SST) and regional-scale climate variability (leading axes of variability in the six regional climate time series) to explain leading modes of biological variability. This analysis took a two-step approach. First, to establish a mechanistic link between basin-scale climate variability and southeast Australian ecosystems, linear models were used to evaluate the ability of the secular trend and leading axes of basin-wide SST variability to explain leading modes of regional climate variability. Models invoking all possible combinations of explanatory parameters were compared with Akaike's Information criterion adjusted for small sample size (AICc; Burnham & Anderson, 2002), and the importance of individual parameters in the best model was estimated with the lmg score, which corresponds to the parameter-specific R^2 value, independent of parameter order in the model (Grömping, 2007). Candidate explanatory variables for biological variability then included only the regional climate modes and the basin-scale variables that were included in the best model of regional climate variability. By using only those basin-scale variables that were strongly linked with regional climate variability, this approach guarded against spurious associations between basin-scale climate variability and regional biological variability. Analysis of biological variability utilized generalized additive models (GAMs) fit with R package "mgcv" (Wood, 2006), and included an autoregressive term (i.e., the response variable at lag-1) to account for the strong autocorrelation typical of biology time series. Smoothing parameters in these models were limited to EDF ≤ 3 in order to prevent model over-fitting and to limit forcing-response relationships to a biologically realistic set of shapes (linear, dome-shaped, sigmoidal). Models invoking all possible combinations of candidate explanatory variables were compared in terms of the GCV score (Wood, 2006) which rewards model parsimony and predictive power in a manner conceptually similar to AIC model selection. Finally, residuals from the best GAM for each biology PC score were assessed for assumptions of normality and independence.

Results

PCA results

Bootstrapping results showed that at least the first ten axes were interpretable for detrended SST data, and the first two axes were interpretable for both the regional climate and biological data sets. Because the study was concerned with only the most important modes of ecological variability, subsequent analysis was limited to the first two axes for each of the three data sets.\

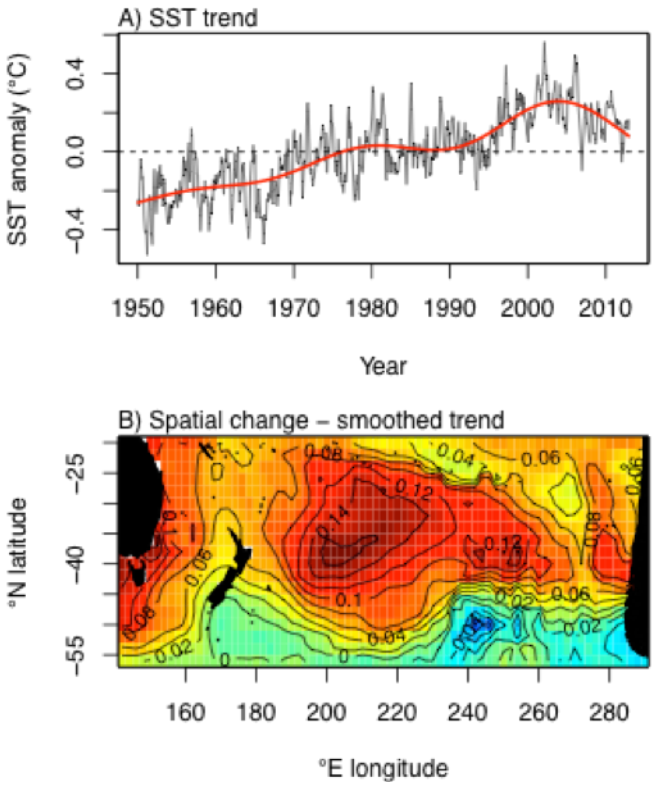

Fig. 5.2 Secular change in South Pacific SST. (A) Basin-wide SST anomalies. Black line indicates monthly anomalies, red line indicates smoothed trend defined by penalized regression splines. (B) Spatial change in SST (°C / decade), 1950-2012, defined by non-parametric regression fit to each cell.

Climate change

South Pacific monthly SST anomalies (SST_{mean}, smoothed with a 36-month running average) showed a complex, rising trend during 1950-2012 (EDF = 8.90, deviance explained = 93.5%, Fig. 5.2A). While the penalized regression spline model suffered from autocorrelated residuals (Durbin-Watson test, $p < 0.00001$), a first-order (linear) GLS model showed a significant trend ($p' = 0.001$), leading to the rejection of the null hypothesis of no secular trend at a basin scale. Spatial patterns in SST increase for southeast Australian ecosystems showed warming on the order of 0.6°-0.8°C during 1950-2012 (Fig. 5.2B).

Table 5.2 Correlations (Pearson's *r*) between SST PCs in this study and leading global SST modes.

	PC1	PC2
MEI	0.80	0.02
NPGO	-0.40	-0.05
PDO	0.65	0.02

Time series of both axes of variability for detrended basin-wide SST ($PC1_{SST}$: 22.7% of total variance; $PC2_{SST}$: 13.7% of variance) showed complex trends, fit by higher-order GAMs ($PC1_{SST}$: EDF = 9.0, deviance explained = 71.9%, $p < 0.0001$; $PC2_{SST}$: EDF = 8.9, deviance explained = 53.4%, $p < 0.0001$; Fig. 5.3). Southeast Australian ecosystems showed moderate negative loadings on $PC1_{SST}$, and moderate positive loadings on $PC2_{SST}$ (Fig. 5.4). The spatial pattern of $PC1_{SST}$ resembled South Pacific loadings of the leading mode of global SST variability (i.e., ENSO; Messié & Chavez, 2011) and was correlated with both the MEI and PDO Index (Table 5.2). While the spatial pattern of $PC2_{SST}$ appeared to resemble South Pacific loadings of the fourth mode of global SST anomalies (i.e., NPGO; Messié & Chavez, 2011), this PC time series was not correlated with the NPGO Index (Table 5.2).

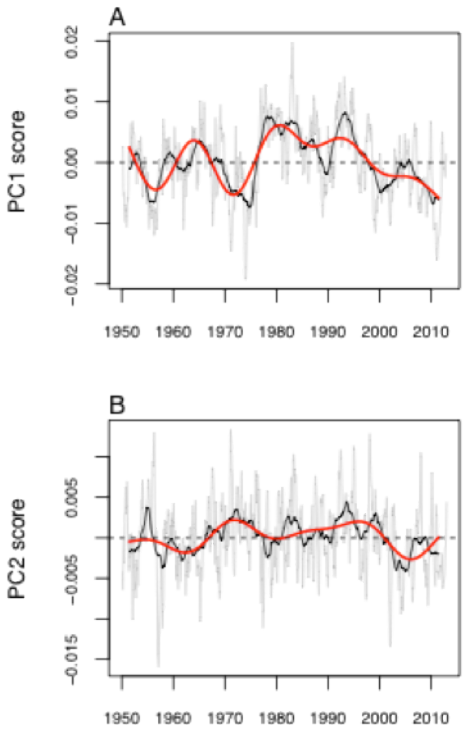

Fig. 5.3 Leading modes of variability in detrended South Pacific SST: (A) $PC1_{sst}$, (B) $PC2_{sst}$. Light grey lines indicate monthly anomalies, mid-weight black lines indicates 36-month running mean, heavy red lines indicate trend defined by penalized regression splines.

The first axis of regional climate variability ($PC1_{reg}$; 34.8% of total variance) was dominated by positive loadings on Maria Island SST and SSS (Fig. 5.5A). $PC2_{reg}$ (24.9% of variance) was dominated by a positive loading on Port Hacking nitrate, and a negative loading on Port Hacking SSS (Fig. 5.5B). The best trend models for both $PC1_{reg}$ and $PC2_{reg}$ invoked linear trends imposed on the noisy time series ($PC1_{reg}$: EDF = 1, deviance explained = 17.7%, $p' = 0.03$; $PC2_{reg}$: EDF = 1, deviance explained = 14.1%, $p' = 0.01$; Fig. 5.6).

The best model for variability in $PC1_{reg}$ ($R^2 = 0.36$, $p < 0.0001$) invoked mean South Pacific SST ($p = 0.0003$, 21.5% of total variability) and $PC1_{SST}$ ($p = 0.003$, 14.9% of total variability). The best model for $PC2_{reg}$ ($R^2 = 0.14$, $p = 0.02$) invoked mean South Pacific SST ($p = 0.01$, 10.7% of total variability) and $PC1_{SST}$ ($p = 0.11$, 3.3% of total variability; Fig. 5.7).

Biological change

Annual estimates for $PC1_{biol}$ and $PC2_{biol}$ scores in 1967 had associated SD values above the absolute value of the time series mean, indicating that too much uncertainty was introduced when estimating missing values for that year. Accordingly, biology PC scores were only analyzed for the period 1968-2010. $PC1_{biol}$ (23.7% of total variance) showed negative loadings on morwong and eastern gemfish recruitment and Montague Island chick counts for sooty and short-tailed shearwaters; and positive loadings on Phillip I. little penguin fledging mass (Fig. 5.8A). $PC2_{biol}$ (21.5% of variance) showed negative loadings Phillip I. little penguin breeding success and fledging mass and eastern gemfish recruitment, and positive loadings on pink ling recruitment and Philip I. little penguin mean laying date (Fig. 5.8B). Complete loadings are presented in Table 5.3.

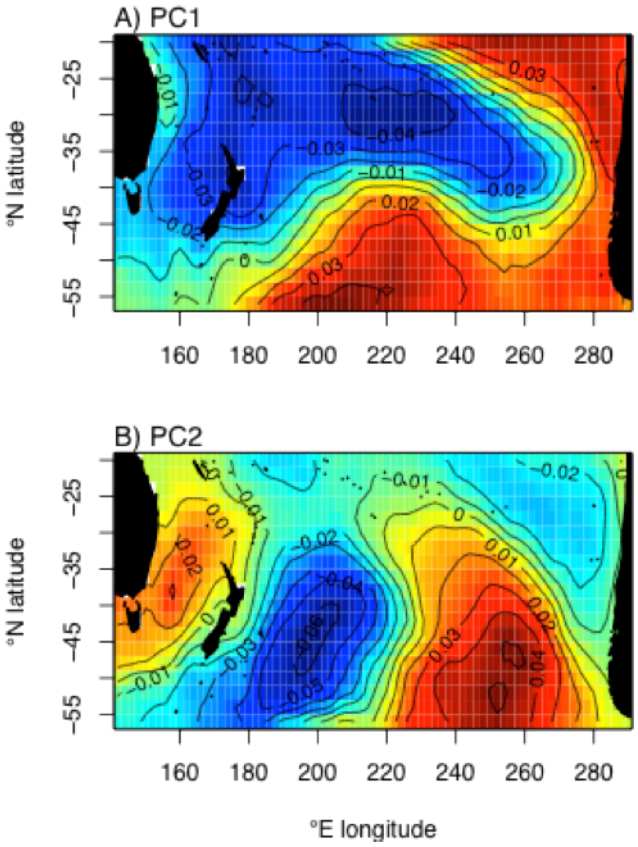

Fig. 5.4 Loadings for (A) $PC1_{sst}$, (B) $PC2_{sst}$.

The best trend model for $PC1_{biol}$ on year showed a non-linear trend (EDF = 1.90, $p < 0.0001$), but the corresponding GLS model did not show a significant quadratic term ($p = 0.09$); a linear trend fit the data well (GLS, $R^2 = 0.71$, $p = 0.0001$; Fig. 5.9A). The best GAM for $PC2_{biol}$, on the other hand, showed no significant trend ($p = 0.20$; Fig. 5.9B).

Resampling of the North Pacific data showed a strong tendency for underestimating EDF when few biology time series were sampled (Fig. 5.10). When $n = 12$ (the number of biology time series used in this study), median EDF = 7.50 (5^{th} and 95^{th} percentile = 1.53, 8.64). At this sample size 80.5% of permutations returned estimates of EDF below the true value from the full data set (8.34). Inspection of the

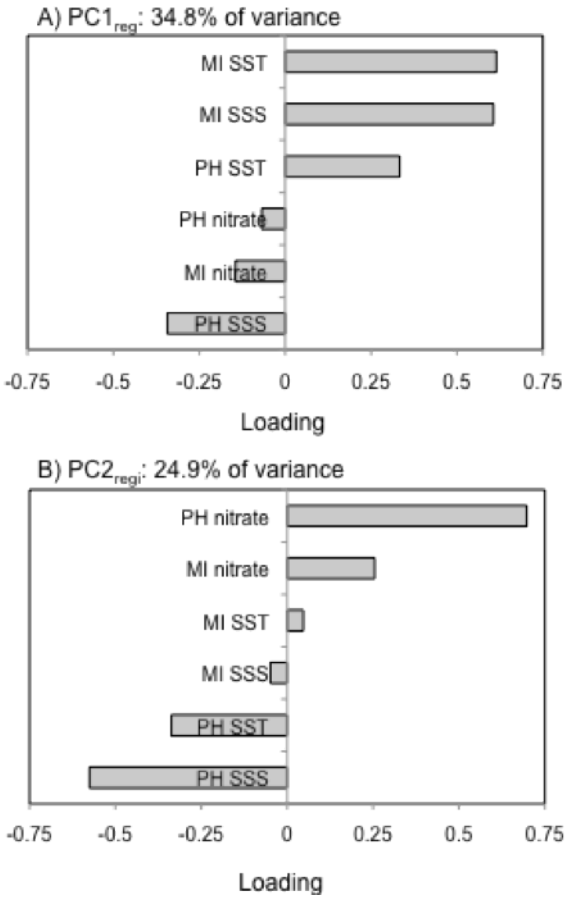

Fig. 5.5 Loadings for leading modes of regional climate variability. MI = Maria Island, PH = Port Hacking.

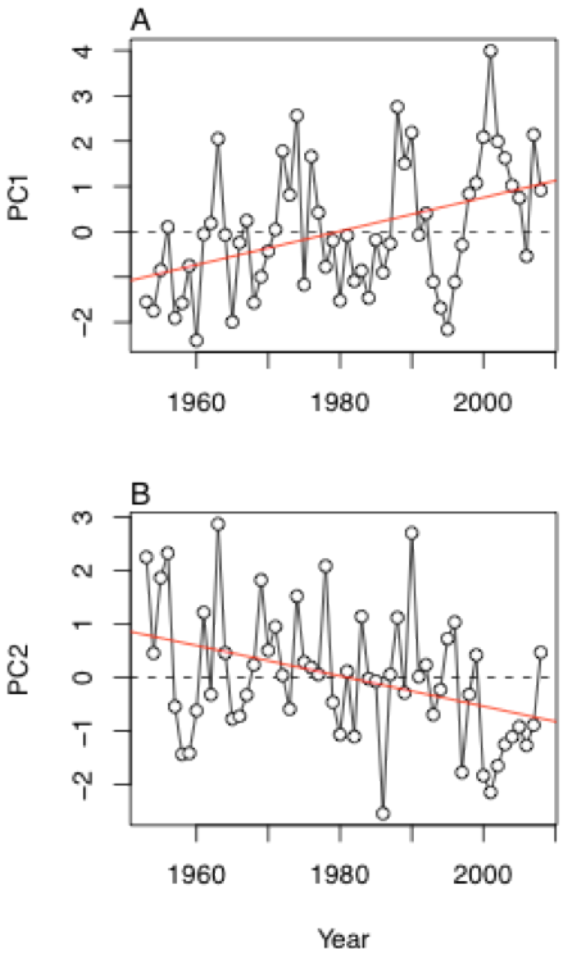

Fig. 5.6 Time series of leading PCs of regional climate. Red lines indicate trends from penalized regression splines; the best model invoked a linear trend in both cases.

EDF 5th percentile curve showed an inflection point around 40% resampling of the North Pacific data (i.e., around n = 25; Fig. 5.10), suggesting a rapid decrease in the ability to detect complex patterns of change with smaller sample sizes.

Climate-biology covariation

Since the best models for variability in regional climate did not include $PC2_{SST}$, this variable was not included as an explanatory variable in analysis of climate-biology covariation. In order to avoid the interpretation problems posed by intercorrelation among explanatory variables (Graham, 2003), model selection for each mode of biological variability was conducted with models invoking either basin-scale climate patterns (SST_{mean}, $PC1_{SST}$) or regional-scale climate variability ($PC1_{reg}$, $PC2_{reg}$). The best autoregressive model for $PC1_{biol}$ invoked SST_{mean} (EDF = 1.94, p = 0.01, deviance explained = 66.9%, Fig. 5.11); the best autoregressive model for $PC2_{biol}$

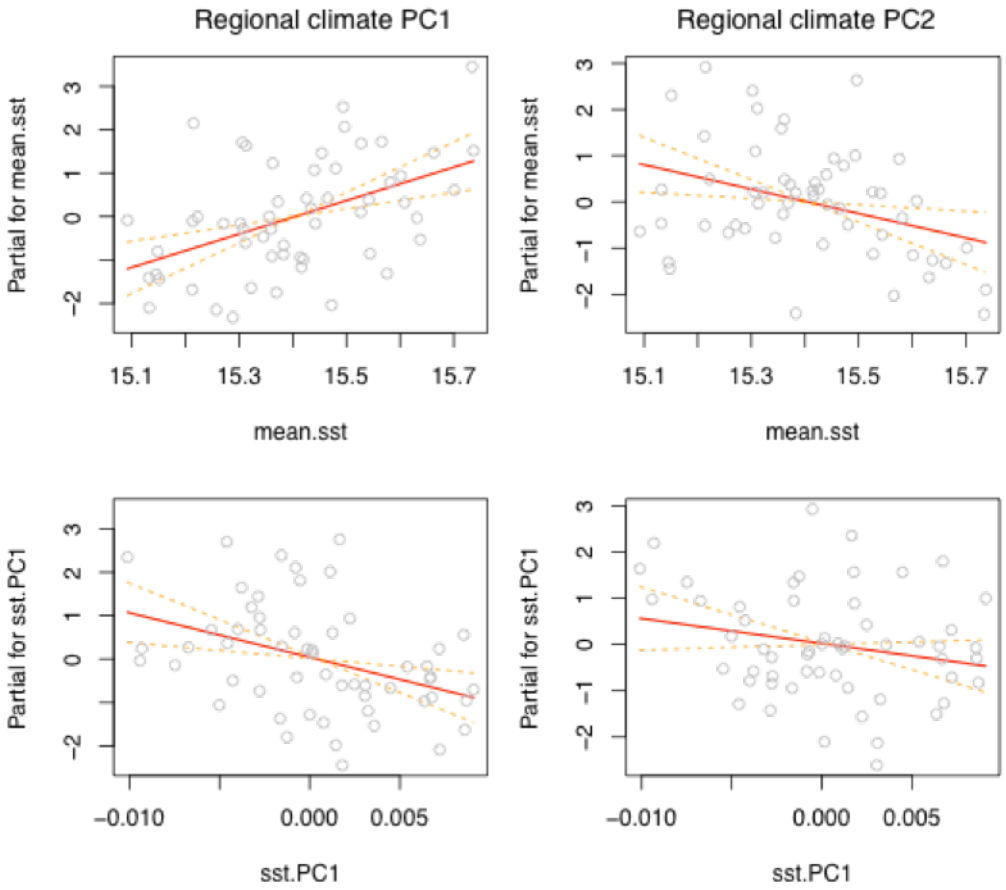

Fig. 5.7 Partial regression plot for effects of basin-scale climate patterns (SST_{mean} and $PC1_{sst}$) on regional climate PCs. Left-hand column = $PC1_{reg}$, right-hand column = $PC2_{reg}$. Solid lines indicate best-fit partial effect, dashed lines = 95% CI.

invoked $PC1_{reg}$ (EDF = 1.00, p = 0.03, deviance explained = 19.2%, Fig. 5.12). Complete model selection results are presented in Table 5.4.

Discussion

Analysis of basin-wide and regional climate parameters in this study suggests the possibility of an important role of low-frequency climate variability in southeast Australian ecosystems. Time series for the two leading modes of variability in detrended South Pacific SST show complex temporal trends (EDF ~ 9) consistent with red noise stochastic variability (Fig. 5.3), and both modes show moderately high loadings in southeast Australia (Fig. 5.4). Furthermore, $PC1_{SST}$ is well correlated with ENSO/PDO variability (Table 5.2, see also the strong jump in $PC1_{SST}$ that occurs around the 1977/78 PDO shift in Fig. 5.3a), and this $PC1_{SST}$/PDO signal is significantly related with both leading modes of regional environmental variability

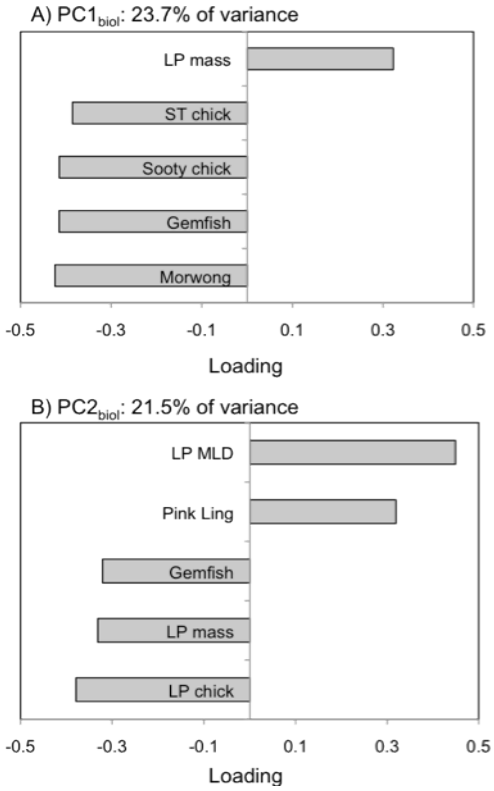

Fig. 5.8 Loadings for first two PCs of biological variability. See Table 5.1 for codes.

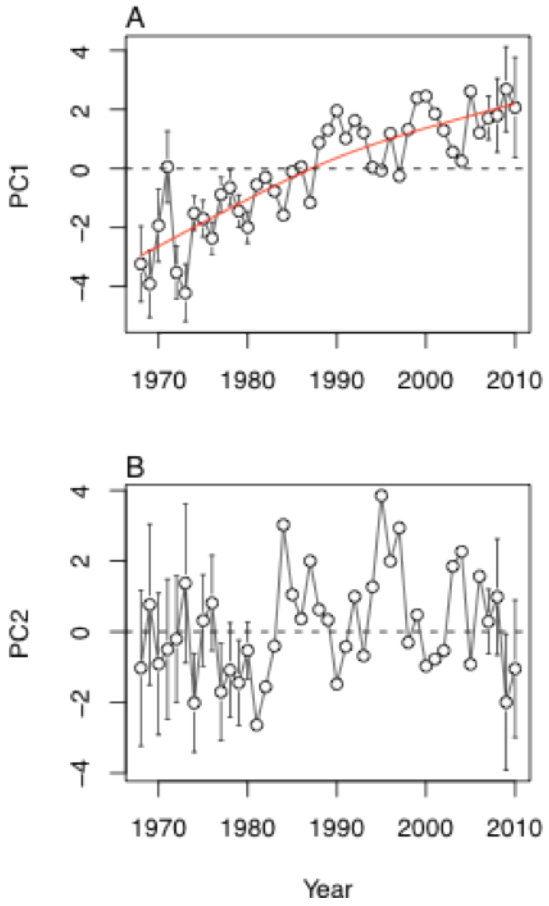

Fig. 5.9 Time series of first two PCs of biological variability. Red line in (A) plots trend in $PC1_{biol}$ defined by penalized regression splines; no significant trend was found for $PC2_{biol}$. Error bars = 95% CI and represent uncertainty associated with estimating missing values.

(Fig. 5.7). However, in spite of this evidence of a role of interdecadal variability in the region, the evidence of a secular trend in regional climate is also strong – both in the linear trends present in the two leading modes of regional climate (Fig. 5.6) and in covariation between regional climate and mean South Pacific SST (Fig. 5.7). This situation is not necessarily different from conditions in Northern Hemisphere systems where red noise or "regime shift" climatic variability has been identified as a leading driver of ecological change, as these systems also experience secular trends in leading climatic (Belkin, 2009; Schwing et al., 2010; Litzow et al., 2014) and biological modes (Spencer et al., 2012; Litzow & Mueter, 2014). Still, the leading modes of biological variability in southeast Australia appear to show either strong secular change with little evidence of multidecadal variability overlaying that trend ($PC1_{biol}$) or noisy variability that was not coherent enough to be modeled with unconstrained non-parametric regression ($PC2_{biol}$; Fig. 5.9). Does this result imply that ecological change in southeast Australian ecosystem is fundamentally different than that in Northern

Hemisphere systems, with climate change producing very rapid secular ecological change that overwhelms any other patterns of low-frequency variability, or

Table 5.3. Complete loadings for first two axes of biological variability ($PC1_{biol}$, $PC2_{biol}$), in ascending order. For code explanations, see Table 5.1.

Time series	PC1 loading	Time series	PC2 loading
Morwong	-0.42	LP chick	-0.38
Gemfish	-0.41	LP mass	-0.33
Sooty chick	-0.41	Gemfish	-0.32
ST chick	-0.39	Whiting	-0.28
Grenadier	-0.24	Morwong	-0.25
Pink ling	-0.20	ST chick	-0.24
LP MLD	-0.04	Warehou	-0.21
Warehou	-0.04	Sooty chick	-0.17
WT chick	0.16	WT chick	-0.07
Whiting	0.19	Grenadier	0.26
LP chick	0.25	pink ling	0.32
LP mass	0.32	LP MLD	0.45

The markedly linear trend in $PC1_{biol}$ during 1968-2010 (Fig. 5.9A) is associated with increasing trends in little penguin fledging mass (positive loading) and declining trends in gemfish and morwong recruitment and short-tailed and sooty shearwater chick counts (negative loadings). These findings are consistent with previous studies documenting trends in life history parameters for the individual taxa involved, although the ability to attribute causes for the observed trends varies widely. The factors responsible for these observed changes appear to be best understood in little penguins, a nearshore species with restricted foraging range that is available for research throughout the year and has been monitored continuously at Phillip Island since 1968 (Dann & Chambers, 2013). A variety of studies have related variability in laying date, reproductive success, mass at fledging and juvenile survival to prey availability mediated by environmental parameters (e.g., Mickelson et al., 1992; Dann et al., 2000; Cullen et al., 2009; Sidhu et al., 2012; Dann & Chambers, 2013). The relationship between basin-scale warming and $PC1_{biol}$ (Fig. 5.11) is consistent with the prey-mediated relationship with increasing SST demonstrated by this body of previous research.

Trends in shearwater chick numbers are more open to various explanations. Climate effects on seabird populations in the southwest Pacific, and southeast Australia in particular, are poorly studied relative to other regions (Chambers et al., 2011). A variety of factors not considered in this study may be acting on the two

Table 5.4 Model selection results for leading modes of biological variability.

Response variable	Explanatory variables	GCV	Δ-GCV	Dev. expl. (%)
$PC1_{biol}$	$PC1_{biol}$ lag1, SST_{mean}	1.21	0.00	66.9
	$PC1_{biol}$ lag1, SST_{mean}, $PC1_{SST}$	1.25	0.04	67.9
	$PC1_{biol}$ lag1, $PC1_{SST}$	1.38	0.17	60.3
	$PC1_{biol}$ lag1, $PC1_{reg}$	1.46	0.25	57.9
	$PC1_{biol}$ lag1, $PC1_{reg}$, $PC2_{reg}$	1.49	0.28	59.3
	$PC1_{biol}$ lag1, $PC2_{SST}$	1.51	0.30	56.3
$PC2_{biol}$	$PC2_{biol}$ lag1, $PC1_{reg}$	2.00	0.00	19.2
	$PC2_{biol}$ lag1, $PC1_{reg}$, $PC2_{reg}$	2.06	0.06	21.4
	$PC2_{biol}$ lag1, $PC1_{SST}$	2.19	0.19	15.2
	$PC2_{biol}$ lag1, $PC2_{SST}$	2.25	0.25	9.0
	$PC2_{biol}$ lag1, SST_{mean}	2.28	0.28	7.8
	$PC2_{biol}$ lag1, SST_{mean}, $PC1_{SST}$	2.31	0.31	15.1

shearwater species loading heavily on $PC1_{biol}$, including environmental variability in distant foraging grounds (Southern Ocean or Antarctica) during the breeding season (Klomp & Schultz, 2000; Cleeland et al., 2014), environmental variability in Northern Hemisphere non-breeding habitat (Napp & Hunt, 2001), plastic ingestion (Carey, 2011; Verlis et al., 2013) and fisheries bycatch (Baker et al., 2002). However, *Ardenna* shearwaters nesting further north on the east coast of Australia are known to experience reduced prey availability and declines in

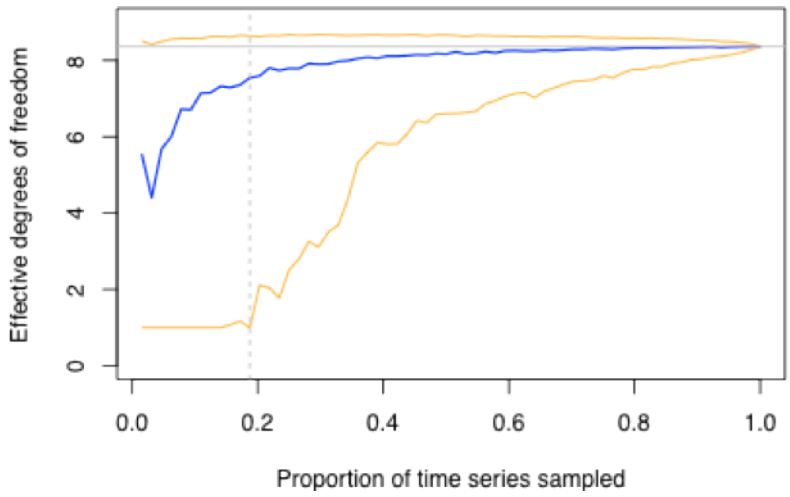

Fig. 5.10 Relationship between sample size and estimated degrees of freedom (EDF) from non-parametric regression analysis of PC1 of North Pacific biology data (Hare and Mantua 2000). Separate regressions were fit to 1,000 random selections (with replacement) of subsamples from n = 1 to *n* = 64 of the population of 64 available time series. Blue line plots median EDF for each *n*, orange lines plot 5th and 95th percentiles. Horizontal grey line plots true EDF for the complete data set, dashed vertical line corresponds to the sample size (*n* = 12) of long-term biology time series available in southeast Australian ecosystems. Note that the tendency to underestimate EDF at low sample sizes will tend to produce conclusions of secular change, rather than interdecadal variability, as the dominant form of temporal variability.

reproductive success during warm SST anomalies (Smithers et al., 2003; Peck et al., 2004), so there is some precedent for population-level response to climate change.

The basic biology for many fishes targeted in the SESSF fishery remains poorly understood (Prince & Griffin, 2001; Rowling, 2001). The two species that loaded heavily on $PC1_{biol}$, eastern gemfish and jackass morwong, have a long history of commercial exploitation, and, for gemfish at least, over-exploitation in the past (Tilzey & Rowling, 2001). Thus, while there is some evidence consistent with environmental regulation of recruitment in, for instance, jackass morwong (Bruce et al., 2001; Jordan, 2001a; Jordan, 2001b; Wayte, 2013), these effects cannot be

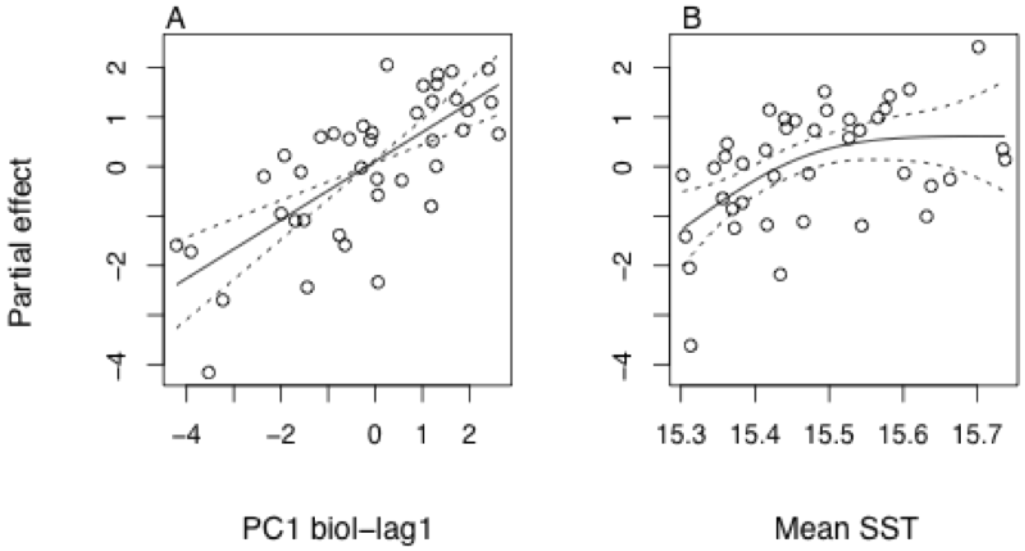

Fig. 5.11 Best GAM for variability in $PC1_{biol}$ (deviance explained = 66.9%): partial effects of (A) first-order autoregressive term; and (B) mean South Pacific SST (SST_{mean}). Solid lines indicate best non-parametric fit with the other term held constant at mean value, dashed lines indicate 95% CI.

disentangled from the effects of fishing – both direct effects on stock size (Tilzey & Rowling, 2001), and through changes to ecological relationships that may produce indirect effects on recruitment (Fauchald, 2010).

The causes of the observed linear trend in $PC1_{biol}$ are therefore likely a mix of different factors, and there is no way to partition observed biological variability among different explanatory variables. This situation is common in biological systems, where ecological complexity typically precludes empirical attribution of observed variability among different drivers (Parmesan et al., 2011). To this extent, observation of strong covariation between the leading axis of regional biological variability and basin-wide warming (Fig. 5.11) is consistent with basin- and global-scale climate change, acting through progressively more local physical processes, as a

mechanism contributing to a community-wide, decadal-scale linear trend. However, formal attribution of observed linear biological change is challenged both by statistical considerations (limited degrees of freedom in the linear trend, intercorrelation among various secular perturbations) and by inherent ecological complexity (Litzow et al., 2014).

Although studies of community-wide responses to climate change are becoming more common (e.g., Ling et al., 2009; Booth et al., 2011; Johnson et al., 2011; Last et al., 2011), marine research in Australia, as in the rest of the world, is still dominated by single-species studies (e.g., Tilzey & Rowling, 2001; Peck et al., 2004; Cullen et al., 2009; Dann & Chambers, 2013). This finding of strong coherence in variability of life-history parameters among ecologically diverse taxa (e.g., a nearshore-foraging, pursuit-diving, flightless seabird; widely-ranging, plunge-diving or surface-feeding volant seabirds; and fishes of the continental shelves) is notable in establishing the presence of strong common trends across southeast Australian taxa that are typically studied in isolation relative to each other. The amount of total variance explained by PC1-2_{biol} in this study (45%) is comparable to the amount of variance explained by the first two axes from community PCA in Northern Hemisphere ecosystems (e.g., 39% in the northeast Pacific, Hare & Mantua, 2000; 42% in the Baltic, Möllmann et al., 2009), although the variance explained in the current study may be inflated by the inclusion of intercorrelated variables in the PCA

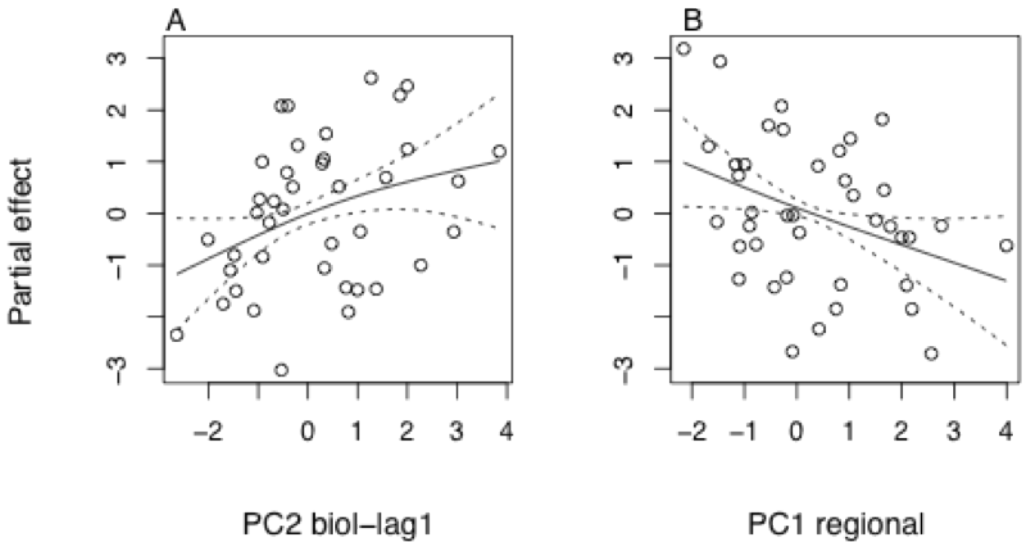

Fig. 5.12 Best GAM for variability in $PC2_{biol}$ (deviance explained = 19.2%): partial effects of (A) first-order autoregressive term; and (B) PC1 of regional climate ($PC1_{reg}$). Solid lines indicate best non-parametric fit with the other term held constant at mean value, dashed lines indicate 95% CI.

(i.e., three parameters for one population of little penguin, data for three *Ardenna* species breeding at a single island). With this caveat in mind, the high proportion of variance explained suggests that the coherent variability that is believed to be characteristic of biological communities (Hsieh et al., 2005) is present in southeast Australian ecosystems, in spite of the ecological characteristics (e.g., oligotrophic waters, high degrees of endemism) that distinguish these systems from their Northern Hemisphere counterparts (Poloczanska et al., 2007).

If southeast Australian ecosystems do show coherent variability similar to that observed in Northern Hemisphere continental shelf communities, does it then follow that low frequency variability in southeast Australia should be characterized by the red noise/"regime shift" interdecadal variability of these other systems? Some anecdotal information suggests the possibility of this sort of variability. Jackass morwong recruitment might have experienced shifts around 1977 and 1988 (Jordan, 2001a; Jordan, 2001b; Wayte, 2013), coincident with shifts in the PDO index (Hare & Mantua, 2000), which is highly correlated with $PC1_{SST}$ (Table 5.2). ENSO variability, which is mechanistically associated with the PDO (Newman et al., 2003), has also been noted as driving biological variability in the region (Johnson et al., 2011). While variability across the biological time series included in the present study is best modeled as a secular process (Fig. 5.9), analysis of the North Pacific data (Fig. 15.0) indicates that the long-term biology data available in southeast Australia do not provide adequate statistical power for detecting abrupt shifts. This situation is part of a widespread problem, as coverage by long-term biological observations is strongly skewed towards terrestrial, rather than marine, ecosystems globally (Richardson & Poloczanska, 2008; Edwards et al., 2010). The development of additional long-term biological observations, perhaps through innovative approaches such as growth chronologies (e.g., Black, 2009) is a necessary step for understanding the true dynamics of change in such systems.

Acknowledgements

We thank Peter Dann and David Priddell for providing access to seabird breeding time series, and Geoff Tuck (CSIRO) for providing fish recruitment estimate time series. Franz Mueter provided much of the R code used in analysis. Climate data were made publicly available by IMOS and the Hadley Climate Centre, University of East Anglia, UK.

Synthesis

Conclusions and Recommendations

The complexity inherent in populations and communities means that "ecological surprises" – outcomes that are well outside the range of possibilities included in formal or informal ecosystem models – are common even in relatively simple, well-studied systems (Doak et al. 2008). Continental shelves are large, complex, open ecosystems characterized by relationships among populations that are multidimensional, diffuse, and context-specific, with available data that tend to cover a minority of community members with incomplete spatial coverage and temporal scales that are adequate for describing only a small subset of potential system configurations. In this difficult situation it is unsurprising that abrupt shifts in continental shelf communities are described with vague terminology (Lees et al. 2006, Overland et al. 2008); deterministic models of the underlying mechanisms are typically far beyond our reach (deYoung et al. 2004a, Andersen et al. 2009, Overland et al. 2010); and there is considerable latitude for disagreement over both the nature and causes of observed ecological change (e.g., the divergent viewpoints included in: Anderson and Piatt 1999, Hare and Mantua 2000, Rudnick and Davis 2003, Worm and Myers 2003, Choi et al. 2004, McClatchie et al. 2010, Frank et al. 2011, MacCall et al. 2012, McClatchie 2012, Zwolinski and Demer 2012, Deyle et al. 2013, Frank et al. 2013, Greene 2013). When post-hoc explanations for observed shifts are produced, even by teams of highly experienced marine ecologists, these explanations are likely to fail with only a few years of subsequent observation (e.g., Hunt et al. 2002, Choi et al. 2004, Choi et al. 2005, Frank et al. 2011, Hunt et al. 2011). This short shelf-life for post-hoc explanations of surprising behavior is again reminiscent of experience in even the most tractable ecosystems, where both models and the intellectual capabilities of humans creating them tend to be inadequate to the task of capturing realistic levels of ecological complexity, and the pattern-seeking behavior of humans in general, and ecologists in particular, leads to a bias towards recognizing consistency and predictability even in situations where pattern and causality cannot be

empirically demonstrated (Doak et al. 2008). Additionally, the transmission and advancement of ideas in this field remains slow. Thus, for instance, random, red-noise processes are very well established in the literature as an appropriate null hypothesis for describing low-frequency climate variability (Rudnick and Davis 2003, Hsieh et al. 2005, Overland et al. 2006, Overland et al. 2008, Overland et al. 2010, Di Lorenzo and Ohman 2013) and this idea has never, to my knowledge, been successfully challenged by comparison with a model of deterministic variability. Nonetheless, the idea that low-frequency climate variability is actually periodic and predictable continues to surface in the ecological literature (e.g., Zwolinski and Demer 2012, Hatch 2013).

Given the considerable difficulties outlined above, what steps might be taken to improve empirical understanding of abrupt shifts in continental shelf communities? The results of this thesis can be generalized into four recommendations for approaching the problem.

First, and most fundamentally, a range of alternate models needs to be considered whenever ecologists are seeking to identify the drivers responsible for observed ecosystem variability (Chapters 1 and 5), to determine the forms that driver-response relationships take (Chapter 1, 3 and 5), or to identify the nature of temporal variability in a system (Chapters 2 and 5). While the evaluation of competing models is standard practice in contemporary ecology (Hilborn and Mangel 1997, Burnham and Anderson 2002), studies of sudden shifts in continental shelf systems frequently rely on testing a single model against a null hypothesis (Möllmann and Diekmann 2012, Spencer et al. 2012).

Second, non-stationary driver-response relationships need to be included in models of ecosystem dynamics (Chapter 3). While the shortcomings of steady-state assumptions for analysis of the control of marine populations have long been recognized (Myers 1998), statistical models rarely include the explicit consideration of non-stationary driver-response relationships. Available methods include threshold generalized additive models (TGAMs; Ciannelli et al. 2004, Ciannelli et al. 2005, Litzow and Ciannelli 2007), which were used in Chapter 3, and state space reconstruction (SSR; Deyle and Sugihara 2011, Sugihara et al. 2012, Deyle et al. 2013).

Third, the results of this thesis support, with important caveats, the application of generic regime shift indicators to continental shelf systems (Chapter 4). The

development of generic indicators potentially represents the most concrete contribution of alternate stable state theory to the management of real ecosystems (Carpenter and Brock 2006). However, the utility of these indicators in actual management situations remains an open question. There is considerable debate among theoreticians concerning their general applicability (van Nes and Scheffer 2005, van Nes and Scheffer 2007, Hastings and Wysham 2010, Boettiger and Hastings 2012a, b, Perretti and Munch 2012, Boettiger et al. 2013, Kéfi et al. 2013), and empirical testing of the idea is at a very early stage of development (Scheffer et al. 2012). In the absence of successful application of generic indicators, managers will continue to need years of observation following an ecosystem perturbation to determine whether community shifts represent transitions to persistent states or ecological transients (Frank et al. 2011). In the case of climate-related variability, the length of observation required to evaluate stability following a putative shift can be determined by comparing interannual variability in climate indices at the ends of time series with that following historical climate shifts (Chapter 2).

Fourth, and last, while detecting the effects of secular climate change in marine ecosystems requires extensive observational data sets (Brown et al. 2011), the detection of complex variability associated with abrupt shifts in systems appears to be even more data-intensive (Chapter 5). Thus, while there are strong statistical relationships between basin-scale climate variability (ENSO and PDO) and regional climate variability in the southwest Pacific, there may simply not be enough long-term time series of biological parameters to know whether continental shelf communities in the region have undergone abrupt shifts related to climate variability of the sort that have been observed in the Northern Hemisphere (Möllmann and Diekmann 2012). In the absence of sufficient long-term data sets, little can be known about the dynamics of change in such a system (deYoung et al. 2004a, Mantua 2004, Brown et al. 2011). In this sense, southeast Australia provides a cautionary example, as the paucity of long-term data sets in that region is more representative of the global situation than is the relatively data-rich northeast Pacific (Poloczanska et al. 2007, Edwards et al. 2010).

Future Directions

> Unfortunately, the complications inherent in multi-species systems almost invariably preclude any quantitative confrontation between theory and data. For multi-species communities, the empirical observations remain largely anecdotal, and the theory remains largely metaphorical.
>
> Robert May (1977)

The results of this thesis suggest three avenues of research that are likely to prove valuable in the future: 1) determining the appropriate null model for community response to external perturbation; 2) balancing the adoption of more flexible statistical approaches with appropriate methods for avoiding potential pitfalls (e.g., model overfitting, inflated Type-I error rates); and 3) developing approaches for dealing with data scarcity and the inherent limitations of observational data.

Alternate stable state theory appears to offer the most promising avenue for developing a general model capable of explaining complex ecological responses to disturbance (Scheffer et al. 2001, Scheffer and Carpenter 2003). In particular, the theoretical prediction that the set of factors regulating communities and populations should be state- or context-dependent (Beisner et al. 2003) offers an appealing advance over statistical models based on assumptions of non-dynamic, steady-state relationships (cf. McClatchie et al. 2010, McClatchie 2012, Sugihara et al. 2012, Deyle et al. 2013). However, the presence of alternate stable state dynamics can be extremely difficult to establish empirically in real ecosystems (Connell and Sousa 1983, Collie et al. 2004, Petraitis and Dudgeon 2004, Schröder et al. 2005). Additionally, the alternate stable state model may be out-competed by more parsimonious explanations, such as lags in community recovery from perturbation that mimic alternative stable states (Frank et al. 2011) and linear responses to perturbation, either with (Di Lorenzo and Ohman 2013) or without (Dudgeon et al. 2010) red-shifted biological responses. Although ecologists are well equipped with model selection approaches that are suitable for identifying the appropriate framework for understanding continental shelf dynamics (Hilborn and Mangel 1997, Burnham and Anderson 2002), data scarcity will be a significant obstacle to answering this question, even in the best-studied ecosystems. Additionally, the complexity of factors regulating marine populations means that the level of understanding required for *a*

priori selection of appropriate parameters to include in candidate models is typically lacking. As a result, this question is unlikely to be resolved soon (Overland et al. 2010).

The challenge of developing models that are capable of capturing ecological complexity leads to the adoption of ever more sophisticated statistical techniques. The exponential increase in computing processing speed, advances in statistics, and the spread of open-source code for applying new statistical techniques have resulted in rapid increases in both the number and complexity of statistical tests that are brought to bear in studies of continental shelf dynamics. The speed at which the

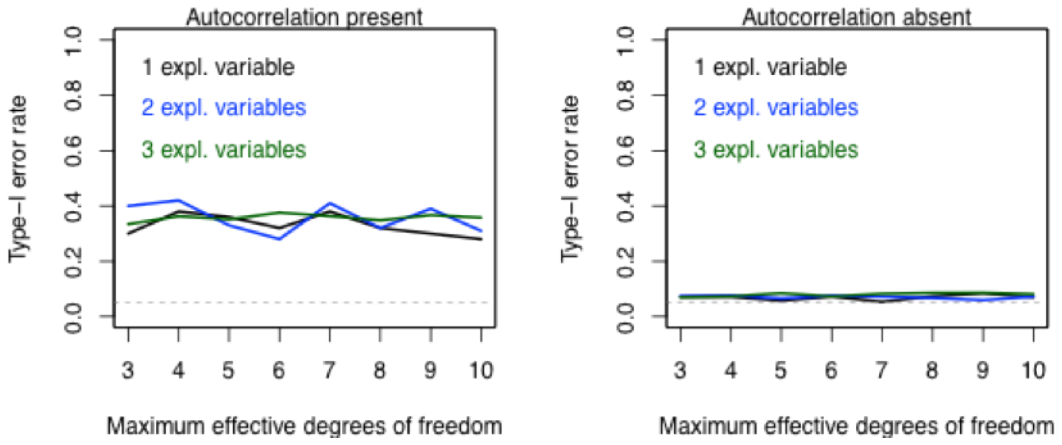

Fig. S.1 The effect of autocorrelation on Type-I error rates in GAM analysis. In the left-hand panel explanatory variables are randomized time series with first-order autocorrelation coefficients (AR1) = 0.95, and response variable is randomized time series with AR1 = 0.6. These levels of autocorrelation are representative for smoothed climate time series and biology time series, respectively, from the northeast Pacific (Chapter 2). In the right hand panel explanatory and response variables are randomized time series with AR1 = 0.01. All time series were 50 years long, and each combination of maximum permitted smoothing (*x*-axis) and number of explanatory variables (1-3) was conducted with 1000 randomized datasets. Dashed horizontal lines indicate $\alpha = 0.05$.

standard of statistical practice has advanced is illustrated by comparing early studies, which often evaluated forcing-response behavior without hypothesis testing (e.g., Mantua et al. 1997, Anderson and Piatt 1999) or with simple cross-correlation analysis (Francis and Hare 1994), versus more recent studies that involve the estimation of hundreds of parameters (e.g., Beggs et al. 2014, Strachura et al. 2014). This increasing model complexity may introduce a number of potential statistical pitfalls. Some of these are well established in the literature, such as unreliable inference in the presence of confounded predictor variables (Graham 2003), inflated Type-I error rates due to multiple hypothesis testing (Verhoeven et al. 2005), and

overfitting, such that the model captures noise rather than fundamental system characteristics (Wood 2010). However, recognition of other important problems invariably lags behind the development and adoption of complex techniques. As an example, consider the relationship between autocorrelation in data and inflated Type-I error rates in GAM analysis (Fig. S1). While appropriate approaches to this problem have been widely adopted for simple linear analysis (Pyper and Peterman 1998, Brown et al. 2011), similar approaches have not, to my knowledge, been published for more complex techniques such as GAMs, TGAMs and SSR. In this thesis I approached the problem by evaluating GAM results with GLS models that account for first-order autocorrelation (Chapter 1), by using a model selection result that does not rely on reporting *P*-values (Chapters 2 and 3) and by estimating first-order autocorrelation directly within GAMs (Chapter 5). While these ad-hoc approaches may be sufficient, publications of a formal comparison of various solutions would aid in standardizing statistical practice and prevent ecologists from relying on "just-so" stories of questionable statistical rigor (Brown et al. 2011). The need for other corrective approaches and formal definitions of statistical best practices will inevitably arise with the continued advance in statistical complexity in the field.

Finally, the quality of available data will determine progress in the elucidation of the complex dynamics of continental shelf systems. Data quality can be measured both in terms of the strength of inference supported (Platt 1964) and in terms of the abundance of biological time series at adequate spatial and temporal scales (Brown et al. 2011). Approaches that strengthen inferences derived from observational studies will be an important step in better understanding of continental shelf dynamics (Brown et al. 2011). Inference may be strengthened by properly designed manipulative studies that test proposed mechanisms (e.g., Estes et al. 1998, Chevaldonné and Lejeusne 2003); however, complex ecosystem dynamics over large spatial scales are typically not amenable to investigation by this approach (Francis and Hare 1994). Since commercial fishing constitutes an ecosystem perturbation that is often planned and carefully documented, fisheries datasets may provide an opportunity to test hypotheses with a quasi-experimental approach (Jensen et al. 2012). The most promising approach for increasing the inference possible from observational data may be studies that make comparisons across multiple ecosystems. Such studies are becoming common in boreal ecosystems sharing similar suites of species (Drinkwater et al. 2009, Link et al. 2009, Mueter et al. 2009) and in upwelling

systems showing similarities in physical forcing and trophic structure (Sydeman et al. 2014). Finally, while improved funding of long-term observation efforts is an important step towards better understanding of continental shelf dynamics (Richardson and Poloczanska 2008, Brown et al. 2011), retrospective datasets may be developed that allow ecological dynamics over the recent past to be better understood. As an example, growth chronologies from bivalves, coral, fish and trees have been useful in elucidating patterns of climate forcing in a variety of marine ecosystems (Gedalof et al. 2002, Black 2009, Black et al. 2011, Gillanders et al. 2012).

To a remarkable extent, the needs for future research outlined here echo those shortcomings noted by Robert May nearly 40 years ago (May 1977). For multivariate situations such as those presented by continental shelf ecosystems, empirical observations confirming theoretical predictions of complex attractor landscapes remain largely anecdotal, and the theory itself remains an abstraction, more a useful metaphor than a working model of natural variability. However, while the central problems remain the same, progress on these issues has been dramatic over the past 40 years, most notably in the ability to incorporate empirical analysis into complex theoretical frameworks and advances in theory that have resulted in explicit, detailed predictions that are amenable to empirical evaluation. These advances have occurred both in simplified one- and two-species systems (Drake and Griffen 2010, Dai et al. 2012, Sugihara et al. 2012), and in more realistic multi-species situations (Hsieh et al. 2005, Carpenter et al. 2011). It is this gradual progression into multivariate settings that provides the most optimism for continued advances in understanding complex ecosystem dynamics over the next 40 years.

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